Biodiversity, altitude and climate change in an Australian subtropical rainforest

Results from the IBISCA-Queensland Project 2006-2010

Edited by Chris J. Burwell, Akihiro Nakamura & Roger L. Kitching

Memoirs of the Queensland Museum | **Nature**

55(2)

ISSN 0079-8835

brisbane | 20 december 2011

Memoirs of the Queensland Museum | **Nature**

Volume 55 Part 2

Biodiversity, altitude and climate change in an Australian subtropical rainforest

Results from the IBISCA-Queensland Project 2006-2010

Edited by Chris J. Burwell, Akihiro Nakamura & Roger L. Kitching

PUBLISHED BY ORDER OF THE BOARD 20 DECEMBER 2011

PO Box 3300, South Brisbane Qld 4101, Australia
Phone 61 3840 7555
Fax 61 7 3846 1226
www.qm.qld.gov.au

National Library of Australia card number
ISSN 0079-8835

COVER: Frode Ødegaard collecting beetles from the understorey of the Antarctic Beech dominated rainforest at the highest elevations of the IBISCA-Queensland altitudinal transect at Lamington National Park, Queensland, Australia. Photo by Jake Bryant / www.envirofoto.com

NOTE

A Guide to Authors is displayed at the Queensland Museum web site www.qm.qld.gov.au/organisation/publications/memoirs/guidetoauthors.pdf

A Queensland Government Project
Typeset at the Queensland Museum
Printed by Kingswood Press
80 Parramatta Rd, Underwood Qld 4119

Queensland Government

qm queensland museum
www.qm.qld.gov.au

PAPERS FROM IBISCA-QUEENSLAND

Preface

In 2003 it was my great pleasure to be invited to participate in the IBISCA-Panama project – an international entomological and botanical collaboration which resulted in about 40 scientists from over 20 countries all descending on a patch of tropical rainforest and exercising their arts in comparing the ground zone with the canopy in that forest. This stimulating and productive experience led me to propose the idea of running a comparable project in south-east Queensland – in our case comparing the diversity of as many taxa as feasible along an altitudinal gradsect within subtropical rainforest. Not only would that greatly increase our knowledge of the flora and fauna of the diversity 'hotspot' close to which some of us live, but it would also give us an indication of what might happen to our biota under various degrees of global warming - each of our altitudinal jumps representing about a 1°C difference in average annual temperature.

After much lobbying and enthusing on my part we were able to obtain the necessary funding to make this idea a reality. With major funds from a Queensland Smart State grant and the Global Canopy Programme, and matching funds from the Queensland Museum, the Queensland Herbarium, Griffith University and Natural Resources Queensland, about 55 scientists from 13 countries visited Queensland over the period 2006-2008, studying a wide range of insect and plant groups, and a set of ecological processes. A number of honours and PhD students also participated as did a prize-winning group of high school students.

This issue of the *Memoirs of the Queensland Museum–Nature* presents some of the first analyses made from these parallel studies. Not all work done is covered and there will be several more articles derived from our studies, including a number of proposed, cross-taxon syntheses. Nevertheless this selection captures the general features of the overarching project, presents a representative range of results and identifies key vulnerabilities within the flora and fauna of our iconic subtropical rainforests.

Roger Kitching

Project Leader, Griffith University

Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project

Roger L. KITCHING[1]

David PUTLAND[2]

Louise A. ASHTON[1]

Melinda J. LAIDLAW[3]

Sarah L. BOULTER[1]

Heather CHRISTENSEN[1]

Christine L. LAMBKIN[4]

1. Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: r.kitching@griffith.edu.au; 2. Growcom, PO Box 202, Fortitude Valley Qld 4006, Australia; 3. Queensland Herbarium, Biodiversity and Ecosystems Sciences, Department of Environment and Resource Management, Toowong Qld 4066, Australia; 4, Queensland Museum, PO Box 3300, South Brisbane Qld 4001, Australia.

Citation: Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011 12 20: Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum – Nature* 55(2): 235-250. Brisbane. ISSN 0079-8835.

ABSTRACT

The IBISCA-Queensland project established 20 permanent plots over an altitudinal range of 300 m to 1100 m above sea-level (d.s.l.) in rainforest within Lamington National Park, south-east Queensland. Four replicate plots were established at each 200 m interval, representing an average temperature change between altitudes of about 1.5°C – a full range of approximately 7.5°C. The project aimed to identify which animal and plant groups are likely to be most sensitive to climate change and which ones can best be used as indicators for monitoring such change. Full vegetation analyses were carried out at each plot and basic climatic and soil data collected. Over an 18 month period insect collections, using a wide-range of trapping methods, were made and specific projects carried out by more than 55 scientists from 14 countries. This paper summarises the history and goals of the project and the general 'IBISCA' model within which it was conceived. Site locations are presented, as is an outline of the specific trapping programme and more specific projects carried out within the broader objectives of IBISCA-Queensland. The strengths and weaknesses of the IBISCA approach are discussed. The first comparative syntheses are anticipated and a broader context for future work is defined. ❐ *IBISCA, Lamington National Park, climate change.*

The estimation of local diversity of terrestrial arthropods presents many difficulties if the goal is a 'complete' or near complete tally of species. Where this has been attempted, processes of gradual discovery and identification over undefined but long time scales have been envisaged. Measures of such alpha diversity are important but, in the face of rapid environmental change through anthropogenic activities from land clearing to global warming, are simply too slow and uncertain to contribute to the development of considered, data-based management responses to such threats. Although measures of alpha-diversity may prove elusive, this is not the case when we attempt to measure location-to-location contrasts in diversity. The comparative method is well suited to estimating species turnover from place to place (beta-diversity), because such turnover is a relative rather than an absolute measure. The standardisation of target taxa and survey methods against a well-thought-out experimental design is one such comparative approach.

Detailed information on arthropod diversity, particularly when matched by coincident botanical and mycological data, potentially provides unparalleled power for detecting beta-diversity in terrestrial ecosystems. The substantial demands associated with sorting large samples of arthropods into many orders, families, genera and species (or their 'morpho'- equivalents) in an age of restricted availability of taxonomic expertise has meant this potential has seldom been fully realised (Kitching 1994). Such multi-taxa approaches, until recently, have been few, extended and generally 'slow to product' (see Basset *et al.* 2003, and references therein).

In 2003, Yves Basset, Bruno Corbara and Hector Barrios initiated a new way of approaching such problems when they established the first IBISCA Project which compared arthropod assemblges in the canopy and ground zone of a tropical rainforest in Panama. Initially an acronym for 'Investigations of the Biodiversity of Soil and Canopy Arthropods', we have applied the name 'IBISCA' to the approach that is characterised now by relatively short-term, multi-scientist and multi-national research projects rather than by the explicit ecological canopy: ground comparisons addressed in the Basset, Corbara and Barrios project. In effect, a multi-skilled team covering expertise in a wide set of target taxa is assembled to work against a fixed experimental design established to address a particular dimension of heterogeneity. The fixed design means that whatever data are generated within the subprojects of individual scientists or teams of scientists can be legitimately compared across taxa and collection methods.

To date, three of the four of IBSCA projects have been conducted in rainforest. A fourth, contrasting project, is on-going in temperate, managed forest in central France.

In Panama, extensive comparisons were made of the diversity within lowland rainforest at ground level with that in the forest canopy overhead (Basset *et al.* 2007). During IBISCA-Queensland (this paper) biodiversity comparisons along an altitudinal gradient were made as a means of establishing a baseline for further studies on the likely impacts of climate change. A similar altitudinal gradient was the basis of IBISCA-Santo held in Vanuatu in 2006 (Tardieu & Barneoud 2007). The further IBISCA project in the Auvergne, France (2008-2010), targeted managed deciduous woodland. Future projects in both rainforest and other woody ecosystems are currently under discussion.

Diversity, Climate Change and the Need for Monitoring

There can be little rational doubt that the Earth is currently undergoing an unprecedented period of rapid warming, almost certainly as a result of elevated levels of so-called greenhouse gases in the atmosphere generated by human-related activities (Intergovernmental Panel on Climate Change 2007). There is growing evidence that this is having direct effects on biodiversity (Steffan *et al.* 2009) through changes of range,

local extinctions, disruptions of interspecific interactions and the modification of ecosystem-level processes. Such climate-driven changes are, of course, superimposed on communities already stressed by other anthropogenic modifications such as land clearing, other forms of pollution and the deleterious effects of introduced species (Department of Environment and Heritage 2004, Westoby & Burgman 2006, Steffen *et al.* 2009). Arthropods are proving to be particularly sensitive monitors of such climate-driven changes, reflecting a complex of features including their short longevities, ectothermic physiologies, relatively low levels of mobility and the tight inter-connectedness of species within communities.

Currently we assume that particular localities on the face of the Earth have associated with them a more or less characteristic set of species. Ecological communities of similar structure recur in places presenting similar environmental conditions within particular biogeographic regions. This statement is the logical basis for the science of community ecology. As climates change, so what we now think of as characteristic climatic 'envelopes' will shift (Westoby & Burgman 2006). Not all taxa that currently occur in a particular place will respond in the same fashion. Some will shift their distributions, others will simply remain where they are until conditions become inimicable for them and they will become extinct, while others may be able to adapt to the new conditions. In addition, species which currently do not occur in a particular location may invade as they follow changes within their particular envelopes of physiological tolerance. The synthetic consequence of this is that the composition of communities will change and re-assortments may well occur, generating new combinations the like of which we have not previously encountered. Of course, this process of re-assortment and subsequent redefinition of ecological communities has occurred frequently through geological time. What is novel in the case of the current episode of climate change is the rate at which we expect this to occur and that, in contrast to changes over geological time, there are self-conscious scientific observers and managers.

Placing these ideas into the pragmatic context of conservation, means that some of our basic precepts have to be re-thought. In Australia, the (often unwritten) baseline for conservation policy is the so-called 1788 approach. This is the notion that we should strive, through policy and management, to preserve as much as possible of the continent in the state in which Captain Cook found it. This has served us well to date. The much-touted CAR (Comprehensive, Adequate, Representative) approach (JANIS Technical Working Group 1995) to the establishment of the national estate of reserved lands is based upon this idea. The 1788 approach assumes that nothing has changed upon the landscape other than what European settlers have done to it physically and biologically. The underlying capability of the land to maintain the set of ecosystems and the biodiversity they contained in 1788 is assumed to be still extant. In fact, processes such as soil erosion, salination, changed drainage regimes and so on may well have imposed irreversible changes upon Australian landscapes but, with a dash of optimism, each can be seen as a set of local events. However, under climate change this is patently an untenable view and management policy needs to adapt accordingly.

Changes in policy settings and management interventions can only ever be as good as the underlying data and scientific understanding on which they are based. Our ability to adapt conservation actions to a changing climate demands adequate and informed monitoring of what changes are occurring across adjacent climates. To do this, we need to know which taxa of the almost unlimited range which we *could* monitor are most likely to show sensitive and interpretable responses to even small amounts of environmental change. We need to identify a 'predictor set' (Kitching *et al.* 2000)

of taxa which we are confident will act as an early warning system for climate-driven impacts upon biodiversity. There is likely to be a unique predictor set of this kind for each ecosystem type. The only logical and robust way to identify such a set of taxa is following an intensive baseline survey. Such a baseline survey and the subsequent identification of predictor taxa has been the goal of the IBISCA-Queensland project, focussing on the extensive remnant rainforests of south-east Queensland.

Altitudinal Gradients and Climate Change

Altitudinal gradients present many different environmental and biological shifts, and are useful tools for understanding ecosystem dynamics. In the last decade the use of altitudinal gradients has developed as they have become recognised as useful study systems, containing many ecotones in a small geographical area. Altitudinal gradients have been used to investigate species turnover and the mechanisms behind patterns in diversity and community structure (Bravo *et al.* 2008, Gagne 1979, Hebert 1980, Lieberman *et al.* 1996, Beck & Chey 2008, Beck *et al.* 2008). Climate change is also being investigated using altitudinal gradients, where gradients in environmental variables such as temperature and precipitation occur in the same area, within the same forest or soil types (Shoo *et al.* 2006). This has been especially relevant in climate change science where altitudinal gradients have been utilised either as analogues for latitudinal climate change, or as a way of examining climate change impact on assemblages along such gradients (Hodkinson 2005).

In summary, altitudinal gradients are of particular value in the study of the interaction between climate and diversity for several reasons:

1. gradients can be chosen which minimize uncontrolled environmental variation so that the impacts of climate are more apparent;
2. adjacent climates can be examined over relatively modest distances making comparative studies practicable; and,
3. an entire set of study sites can be established within a particular biome (such as rainforest).

Climate change will elicit a complex array of responses, which makes it difficult to form predictions or generalisations about future impacts based on the responses of any one study group. Many studies have used either latitudinal or altitudinal transects as gradients to examine how the distribution of groups, such as insects, are changing in response to climate change (Andrew & Hughes 2005, Botes *et al.* 2006, Inouye *et al.* 2000, Progar & Schowalter 2002). A number of abiotic factors, such as temperature and precipitation, change consistently with altitude and these factors influence the altitudinal distribution of arthropods. One of the major criticisms of altitudinal studies has been that the environmental and biological factors may all be inter-correlated. Conversely, these correlations give altitudinal gradients potential to explore these physical and biological factors and make predictions about how they will change and how biota will respond.

Temperature lapse rate. Temperature decreases as elevation increases; dropping by about 1.5°C in dry air for every 200 metre increase in elevation (Jacobson 2005). Fundamentally this is because air expands as it rises and loses heat in consequence. This is basic physics. The lapse rate will change only if there is water condensation in the air, or local addition or removal of heat from either above or below. From above heat exchange may occur due to solar radiation on the one hand, or conduction into overlying cold air, in the other. From below, conduction may occur to or from a soil surface having a different temperature. In any particular environment, therefore, local conditions such as seasonality, diurnality, topography, aspect, precipitation and cloud level (Lookingbill & Urban 2003) may effect lapse rate but these effects are likely to be minor.

The spatial relationship between atmosphere and surface factors is complex and is expected to be altered by climate change (Pepin 2001). Temperature lapse rate may decrease with climate change because of increased condensation of

water from the more humid atmosphere: accordingly, high altitude sites are likely to experience warming at a greater rate than lowland sites (Foster 2001). Arthropods will, almost certainly, be strongly influenced by temperature, which can affect the distributions of both insects and their host plants.

Precipitation. Precipitation generally increases with altitude (Fowler *et al.* 1988). Moisture levels are highest where the cloud cap sits due to horizontal precipitation through direct contact between cloud and soil or vegetation. It has been suggested that climate change is predicted to increase the average cloud cap altitude on mountain tops. Temperature increases will change the altitude at which water vapour will condense, altering moisture levels dramatically and, potentially, drying cloud forests (Pounds *et al.* 1999, Still *et al.* 1999, Williams *et al.* 2003). This 'conventional' analysis to some extent understates the complexity of water/atmosphere interactions and contradicts received wisdom on temperature effects (see above). A warmer 'greenhouse' world will hold more water as vapour in the atmosphere, potentially increasing the facility for cloud and mist formation. Higher levels of water held in the atmosphere will also modify the adiabatic lapse rate to as little as 0.15°C per 100 m (American Meteorological Society 2000) with, presumably, consequential effects on the average level of the cloud base. The observed drying of cloud forest may at least in part reflect changes in local water dynamics as underlying lowland forests are cleared (Lawton *et al.* 2001).

Altitudinally, precipitation regimes can be confounded by local factors such as seasonality and topography (Henry 1919). Arthropods can be affected physically by precipitation, for example, through desiccation due to drought, or indirectly through effects on host plants (Schulze *et al.* 2001). Variability of precipitation patterns has a direct impact on arthropod species' abundance and reproductive success, with some species exhibiting greater success with increased rainfall whilst others are more successful during dry periods (Speight *et al.* 1999).

THE IBISCA-QUEENSLAND PROJECT

We elected to study an altitudinal gradient in order to examine changes in biodiversity across a set of adjacent climates driven by the changes in altitude. This involved the study of the biodiversity of sets of replicated sites at five different altitudes above sea level. These altitudes represent a series of five adjacent climates each separated by 200 m of altitude (equivalent to approximately 1.5°C steps in average temperature regime).

Lamington National Park contains by far the largest remnant of undisturbed rainforest within the Australian subtropics. The region is also identified as a national 'hotspot' of biological diversity and is known to be a point of overlap between characteristic temperate south-eastern biota and more tropical northern elements (the MacPherson-Macleay overlap zone; Burbidge 1960). The Lamington National Park is also one of the properties making up the 'Gondwana Rainforests of Australia' World Heritage Area (see Kitching *et al.* 2010, for a comprehensive set of general accounts).

Based on the kraznozem soils of old Tertiary volcanoes, the 23000 ha of the Lamington National Park is dominated by rainforests ranging from rich warm subtropical vegetation to the species-poor forests of the highest elevations ('cool temperate rainforest') (Hutley, 2006). Intermixed with the dominant krasnozem soils are areas of more acidic rhyolitic soils which are poorer in nutrient and drainage but which also maintain rainforest in wetter areas. The IBISCA study was restricted to areas of krasnozem soils. We were able to establish a set of twenty sites representing replicated sampling points at five elevations along an altitudinal gradient within continuous, undisturbed rainforest within a single major catchment of the park. All sites were located on the same geological substrate.

Over a series of major field excursions, we sampled the vegetation, fungi and invertebrates along this gradient throughout the year. In addition, a number of parallel subprojects examined specialist taxa, collecting procedures or ecological processes.

The project set out to collect baseline information from the region and to use it to test the following hypotheses:

1. there is an altitude-related turnover in biodiversity operating within the forest under examination;
2. some taxa, or elements within taxa, will show more dramatic or clear-cut changes along the altitudinal gradient than will others;
3. these taxa have potential for monitoring future changes in climate;
4. ecological processes which are driven by particular taxa will change in degree or intensity along the altitudinal gradient;
5. species or groups of species at the highest altitudes are, potentially, most at risk under scenarios of future global warming; and,
6. a monitoring approach based on a thorough baseline assessment along an altitudinal gradient is likely to provide a powerful future management tool.

These activities comprised the IBISCA-Queensland Project.

The project was conceived following Kitching's participation in the earlier IBISCA-Panama project and developed during a follow-up visit to the USA as a Queensland-Smithsonian Fellow. Griffith University in partnership with the Queensland Museum, Queensland Herbarium, SEQ Catchments, the National Parks Association of Queensland and the Global Canopy Programme (Oxford, U.K.) developed the proposal which subsequently received major support from the Queensland Government under the National and International Research Alliances Program. Matching funds from the participating partners allowed the first field expedition to be mounted in October 2006.

In total, more than 50 research scientists and students participated in the project assisted most ably by over 70 volunteers. The scientists originated from 14 different countries.

DESIGN AND METHODS

Site Selection, Location. Lamington National Park was established in 1915 to preserve an area of upland forest located just north of the Queensland/New South Wales state border. With some later additions it now comprises 23000 ha dominated by broad-leaved rainforest. Extensive and important areas of dry and wet sclerophyll forest and sclerophyllous heath also occur within the park. The physical and current climatic environment of the region is described by Strong *et al.* (2011). The vegetation has been studied extensively over many years (Hopkins 1975, Olsen & Lamb 1988, McDonald & Thomas 1990, Laidlaw 2009). Comparable ecosystems in New South Wales are described at length by Floyd (1990).

Within the national park one of the principal catchments is that of Canungra Creek which rises close to the border escarpments and drains to the north. It has western and eastern branches which converge at about 400 m elevation. This catchment has a relatively uniform substrate (see Strong *et al.* 2011) and is also accessible over much of its length. Accordingly this was the location of choice for our study.

Within the West Canungra Creek catchment we were able to identify an extensive area of continuous rainforest vegetation from the extreme northern limit of the park at about 300 m a.s.l. to the Queensland/New South Wales border at about 1100 m a.s.l. Along this gradient we established five sets of four sites at approximately 300, 500, 700, 900 and 1100 m a.s.l. respectively (Table 1, Figure 1). This design regards the five altitudes as treatments with four more or less independent replicate sampling sites within each treatment. All sites were located within a

single catchment and hence, in a strict statistical sense, our results lead to conclusions only about forest within this catchment. The forest types within the catchment, however, are examples of widely distributed subtropical rainforests and we are confident that the baseline information we have will have wide relevance (see Discussion for further comments).

The twenty study sites were chosen against the following criteria:

1. each site should be accessible on foot;
2. each site should allow the establishment of a permanently marked central 20 m × 20 m vegetation plot;
3. each site should be within undisturbed rainforest;
4. each site should have the same soil type and aspect;
5. sites should be at least 300 m apart at each elevation; and,
6. sites should not be riparian.

Naturally such a set of requirements could not be wholly prescriptive but, as shown in Table 1 and Figure 1, these requirements, by and large, were met.

TABLE 1. Labels, locations and altitudes of the 20 sites of the IBISCA-Queensland transect.

Designation	Latitude	Longitude	Altitude (m a.s.l.)
IQ-300-A	-28.148	153.137	267
IQ-300-B	-28.155	153.139	282
IQ-300-C	-28.151	153.138	260
IQ-300-D	-28.142	153.133	248
IQ-500-A	-28.216	153.142	560
IQ-500-B	-28.213	153.103	514
IQ-500-C	-28.210	153.187	474
IQ-500-D	-28.207	153.137	471
IQ-700-A	-28.188	153.121	746
IQ-700-B	-28.192	153.124	775
IQ-700-C	-28.193	153.128	748
IQ-700-D	-28.204	153.129	748
IQ-900-A	-28.234	153.141	904
IQ-900-B	-28.238	153.145	950
IQ-900-C	-28.240	153.149	944
IQ-900-D	-28.227	153.131	920
IQ-1100-A	-28.258	153.159	1141
IQ-1100-B	-28.259	153.162	1142
IQ-1100-C	-28.260	153.167	1106
IQ-1100-D	-28.262	153.170	1140

Environmental Data Collection. As a basic part of the project, climate stations were established at each altitude. In addition temperature and humidity data-loggers were located at both ground level and in the canopy at each of the twenty sites. A single set of soil samples was taken within each of the twenty sites and submitted to a series of chemical and physical analyses. Strong *et al.* (2011) present details of these methodologies and the results obtained.

Vegetation and Fungal Surveys. As each site was established, a central galvanised steel post was erected to which a permanent location label was welded. The exact location and altitude of this central locator post was recorded (Table 1). A baseline vegetation plot was established comprising a 20 × 20 m square quadrat centred on the reference post. Within that area, all trees greater than 5 cm dbh were marked, measured and identified. In addition, a list of all vascular plants occurring within the plot was made. The results of these vegetation surveys are presented by Laidlaw *et al.* (2011).

In addition to these surveys of the vascular plants, Dr Elizabeth Brown (Royal Botanical Gardens, Sydney) carried out surveys of bryophytes. Further, the Queensland Mycological Society, under the leadership of Nigel Fechner (Queensland Herbarium), undertook surveys of fungal fruiting bodies based in and adjacent to the sampling sites.

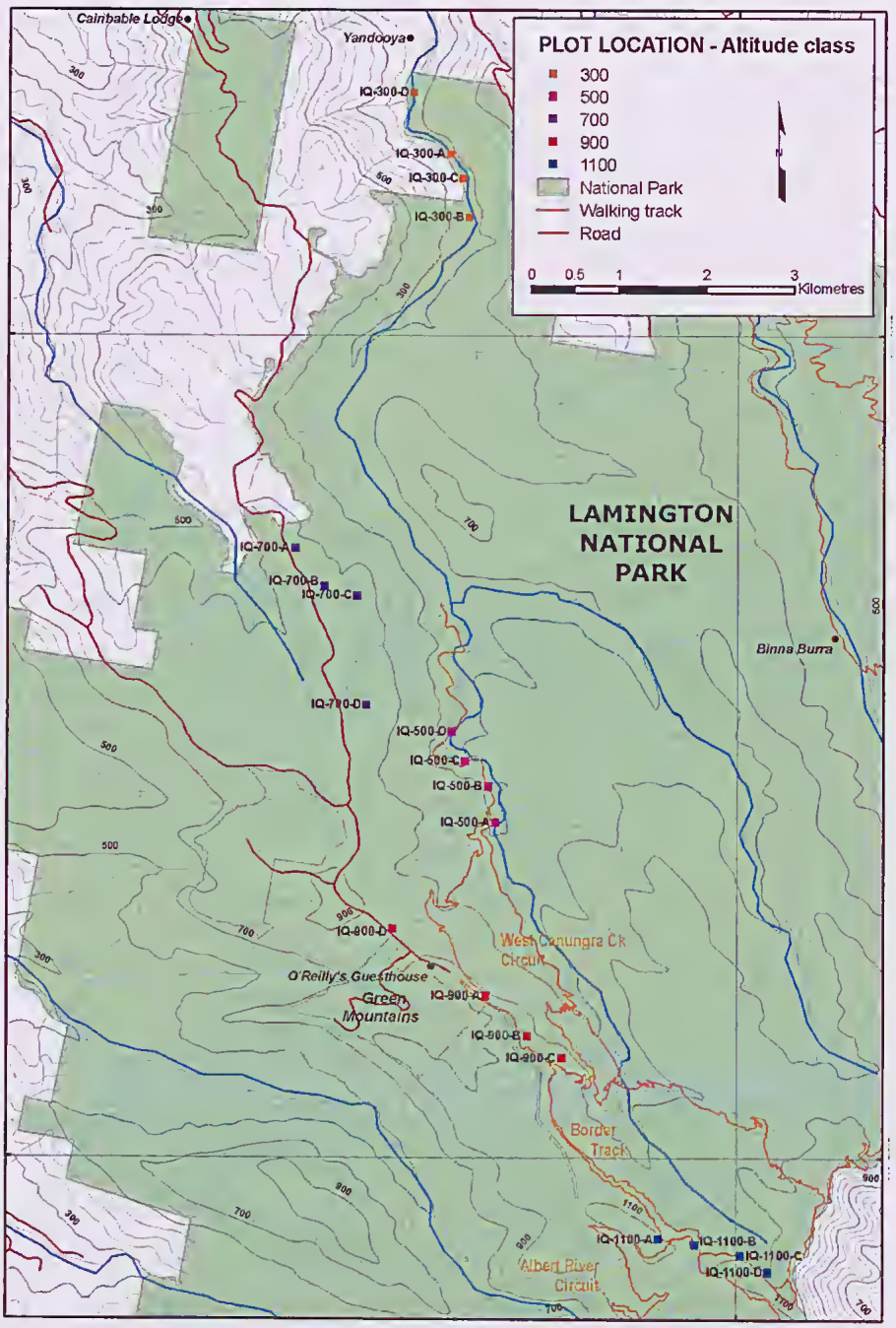


FIG. 1. Map showing the location of the IBISCA-Queensland transect and the distribution of plots along it (prepared by Rosemary Niehus, Queensland Herbarium).

TABLE 2. Trapping and projects carried out during IBISCA-Queensland (§ 700-1000 m only, at 50 m altitude intervals

Trapping Method/ Project	Pre-Project	Oct-06	Jan-07	Mar-07	Jul-07	Jan-08	Scientist(s)
Foundation							
Vegetation surveys	✓	-	-	-	-	✓	Laidlaw, Macdonald, Hunter
Climate data	-	throughout					Putland, Kitching
Baseline methods							
Malaise traps	-	✓	✓	✓	✓	-	Lambkin
Flight intercept traps	-	✓	✓	✓	✓	-	Monteith
Light traps	-	✓	-	✓	-	✓§	Kitching, Ashton, Maunsell
Pitfall traps	-	✓	✓	✓	-	-	Staunton, Putland
Bark spraying	-	✓	-	✓	✓	✓	Burwell, Nakamura, Wright, Thompson
Canopy knockdown	-	✓	-	-	-	-	Floren
Litter extraction	-	✓	✓	✓	-	-	Putland
Yellow pan traps	-	✓	-	✓	-	-	Putland
Other projects							
Beating	-	✓	-	✓	-	✓	Ødegaard
Canopy leaf quality & herbivory	-	-	-	-	-	✓	Kitching, Putland, Laidlaw, Hunter
Thysanoptera studies	-	✓	-	✓	-	-	Mound, Tree
Hole-nesting insects	-	✓	✓	✓	-	-	Morris
Dung-beetles	-	✓	✓	✓	✓	-	Monteith, Menendez
Bark fauna	-	✓	-	✓	-	-	Schmidl, Bittner
Ants & herbivory	-	✓	-	-	-	-	Bito, Novotny
Host specificity in herbivory	-	-	-	-	-	✓	Bito
Social insect surveys	-	✓	-	✓	-	-	Corbara, Burwell, Leponce, Orivel, Roisin, Delsinne
Spider surveys	-	✓	✓	✓	✓	-	Raven, Baehr
Dolichopodidae	-	✓	-	✓	-	-	Bickel
Pollination studies	-	✓	✓	✓	-	✓	Boulter
Galls in the canopy	-	✓	-	✓	-	-	Barbosa da Silva, Ribeiro
Mollusc surveys	-	✓	✓	-	-	-	Stanisic, Carless
Xylophagous Coleoptera	-	✓	-	-	-	-	Curletti
Earthworms	-	✓	-	-	-	-	Dyne
Flower/insect interactions	-	✓	-	-	-	-	Frame
Geometridae	-	-	-	✓	-	-	Leveque
Mite studies	-	✓	-	✓	-	-	Walter, Proctor
Fungal surveys	-	throughout					Fechner, Queensland Mycological Society
Moss surveys	-	-	-	✓	-	-	Brown
Decaying wood biomass	-	-	-	-	-	✓	Putland
Soils	-	-	-	-	-	✓	Putland

Baseline Trapping and Individual Projects. Drawing on experience from previous IBISCA projects, it was decided that a core activity of IBISCA-Queensland would be repeated sets of trapping using a range of standard trap designs. These are summarised in Table 2 which also indicates in which seasons they were applied.

The basic trap designs used are described in detail in Kitching *et al.* (2005). Most trapping methods were applied on at least three occasions in an attempt to capture seasonal variability. Canopy knockdown using pyrethrum insecticide was applied only in October 2006. Further details of the duration and disposition of these traps are presented by individual authors elsewhere in this special issue.

Responsibility for these standard trapping regimes and the processing of the catches has been a central responsibility of the Project Team. In addition, participating scientists carried out a wide range of more specialised surveys across the IBISCA sites which, on occasion, involved using duplicate sets of traps or other additional trap designs. These are summarised in the lower part of Table 2.

Labelling and Databasing Protocols. Participants from the Queensland Museum (primarily Christine Lambkin and Karin Koch) developed a detailed set of protocols for labelling and databasing the collected samples. Every sample collected was given a unique number for ease of subsequent tracking. Numbers were attached to recording sheets for participants to add to samples collected in the field. Ultimately, some 4375 such sheets were completed by participants in the project, and the localities entered into the Queensland Museum database. Standard specimen labels were prepared for all samples, and made available to all participants through the IBISCA-Queensland website. Also provided on the website were duplicate sample labels, sorting sheets, identification labels and all sample data for the October, January, March and July surveys. To date, over 8,500 identified specimens are registered in the database. These standardised methods and the project-wide database were used by all participants and all sub-projects. This consistency in procedures across the project provides the ability to combine data in novel ways to explore complex patterns, and the benefits of this approach are displayed in many of the papers presented in this volume.

Sorting and Curating. In the first instance, based on priorities established at a scientific workshop in April 2007, samples have been partly sorted to seven major arthropod groups and the residual catch. To this end all Heteroptera, Thysanoptera, Coleoptera, Diptera, Hymenoptera - ants, Hymenoptera - non-ants, and Araneae have been sorted and removed from all baseline methods for all seasons, with the exception of light traps and samples from March 2007 for which sorting is still ongoing. Sorted individual groups have been dispatched to specialist taxonomists for further sorting. In other cases, selected taxa and sampling methods have been prioritised by particular workers. Lepidoptera from light traps, Diptera from Malaise traps, a range of taxa from beating samples, and beetles from pitfalls, bark sprays and intercept traps have been targeted. The outcomes of some of these endeavours are presented in this special issue. We also are in receipt of specific returns on selected taxa such as Collembola, Thysanoptera and Tephritidae.

This Volume. This special issue of the *Memoirs of the Queensland Museum* presents basic data from the IBISCA-Queensland project that became available by mid-2009. It cannot be a complete account of our results – indeed, the idea of 'completeness' for such an extensive and multi-dimensional project is elusive. Nevertheless, it presents early results for what is a major study of its kind in Old-World rainforests. For Australasian rainforests it bears comparison only with the IBISCA-Santo

(Vanuatu) (Tardieu & Barneoud 2007) project which was carried out between the first two major field trips of the IBISCA-Queensland project. The basic idea and design of the overall IBISCA Programme is presented in this paper. Strong *et al.* (2011) outline the climate and soil properties of the study sites. Two papers summarise the vegetation characteristics of the altitudinal gradient. Laidlaw *et al.* (2011) present the characteristics of the vegetation with special reference to altitude-to-altitude turnover. Boulter *et al.* (2011) summarise the reproductive phenology of the flora. The remainder of the papers refer to the arthropod surveys carried out within or adjacent to the study sites. Boulter *et al.* (2011) present results on the ordinal distribution of insects encountered in Malaise and flight intercept traps. Ødegaard and Diserud (2011) summarise results obtained from beating surveys of the sites for Coleoptera, Hemiptera and Mutillidae. Staunton *et al.* (2011) compare patterns encountered among three predatory taxa – the ants, predatory beetles and spiders. A series of papers tackle single taxa encountered along the transect. These include the Formicidae (Burwell & Nakamura 2011), the moths (Ashton *et al.* 2011), Collembola (Greenslade *et al.* 2011), thrips (Tree & Mound 2011), orsolobid spiders (Baehr *et al.* 2011), spiders of the genus *Opopaea* (Araneae, Oonopidae) (Baehr 2011), Diptera collected using Malaise traps (Lambkin *et al.* 2011). Finally two papers tackle insect/plant interactions. Ribeiro and Barbosa (2011) examine vertical profiles of the occurrence of galls along the altitudinal transect and Bito *et al.* (2011) describe the interactions between ant abundance and herbivory at different altitudes.

DISCUSSION

Towards Syntheses

The underlying scientific imperative for this project has been to obtain information on the way the diversity and distribution of a variety of plant and invertebrate taxa change along a continuous altitudinal gradient within subtropical rainforest. This is basically an exercise in the measurement of beta-diversity from altitude to altitude within the forest. As such it is quintessentially a comparative exercise. This is by no means the first such comparative exercise which has been carried out. However, the advantage presented by the IBISCA methodology is that all data returns can legitimately be laid alongside each other and subjected to rigorous comparative analysis. The underlying common experimental design to whatever target taxa are studied, using whatever trapping methods, gives a statistical power to the analyses which unplanned meta-analyses cannot possess. This having been said, what we present in this volume is a series of single (or few) taxa descriptions based on one or a small number of trapping methods. As such we cannot claim yet to have fulfilled the promise of the IBISCA methodology.

What will emerge from these studies are synthetic outcomes in which subsets of data combining results for different taxa and/or trapping methodologies are combined to answer questions the importance of which will transcend the patterns observed for any one approach. The set of such synthetic outcomes is open-ended but we anticipate it will include:

1. IndVal (Dufrene & Legendre, 1997) analyses for a wide range of taxonomically defined data-sets to define a statistically useful multi-taxon 'predictor set' for the future monitoring of the impact of climate change on diversity;
2. comparative analyses of the relative importance of 'common' and 'rare' species in the detection of pattern in rainforest biological assemblages (see e.g. Gaston 2008);
3. key differences and similarities within altitudinal patterns (and, by inference, sensitivity to climate change) in taxa belonging to different guilds (herbivores vs predators; detritivores vs herbivores; ground dwellers

vs canopy dwellers, etc); and,

4. the utility and efficiency of different sampling methods in obtaining 'rapid' assessment of biodiversity change (cf. Kitching *et al.* 2001).

Other syntheses will no doubt emerge as our results stream matures.

Only One Catchment?

There is no avoiding the fact that our current set of results relate to one catchment within a single national park exhibiting but one set of vegetation characteristics. If it takes a project of this magnitude to characterise the biodiversity of a single catchment within a single set of ecosystems within just one geographical region, is there any realistic likelihood that we can develop general tools for understanding biodiversity pattern and its likely response to climatic (or any other form of environmental) change? The answer is a resounding, yes!

The value of the set of results which have emerged and will continue to emerge from the IBISCA-Queensland project is that they represent a yardstick against which other less complete sets of data can be compared and assessed.

Building on the patterns observed in particular taxa as measured by specified sampling protocols within the IBISCA-Queensland study, we can examine other locations with much greater efficiency and focus. We add hastily that such efficiency and focus is now possible only because of the breadth and comprehensiveness of the IBISCA-Queensland project. A first step forward is to expand sampling within the Lamington region – to other catchments, other aspects, other substrates, to validate (or otherwise) the generality of the project's results. Already, based on ant work, we know the general altitudinal patterns hold up within other catchments and yet are modified, probably due to overland flow of colder, heavier air close to active drainages (Burwell & Nakamura 2009; C. Burwell pers. comm.). This generality and its topographic modifications needs confirmation using other contrasting taxa (such work is in progress) yet can be very focussed and clinical, based on the outcomes predicted by the IBISCA-Queensland results.

The fact remains, nevertheless, that baseline surveys such as those undertaken in IBSICA-Queensland will be necessary for other key ecosystems. However robust are the patterns observed in subtropical rainforest within Lamington National Park, it is unreasonable to expect them to be anything other than a striking contrast to results we might expect along an altitudinal gradient within sclerophyll woodland or even fully tropical rainforest, let alone grassland or savannah.

'Missing' Taxa

One of the underlying principles behind the IBSICA-Queensland project was that it provided a means by which the scattered resources represented by the taxonomic establishment could be joined in a single enterprise to produce results far beyond those which any one specialist, collaborating with ecologists in the field, could hope to produce. Nevertheless, there is a national and global dearth of practising taxonomists and this shortage must be further viewed against our growing appreciation of just how diverse is life on Earth, and the appalling rates at which it continues to disappear. So how comprehensive was the taxonomic coverage achieved by the IBISCA-Queensland project. And how significant are any short-comings?

We achieved reasonable coverage of the Lepidoptera (although many families of micro-lepidoptera remain unstudied). Coleoptera also were adequately dealt with, in no small part due to the efforts of our Norwegian and German colleagues. Diptera have been analysed down to family level and several specialists are pursuing further resolution on selected families. The other mega-Order, the Hymenoptera, was covered patchily. We had five project specialists focussing on one family: the Formicidae. The project was fortunate to have specialist parti-

cipation for Collembola, Thysanoptera and Araneae. Acari also received some attention but, of course, this in no way matched (or could have matched) their vast known and anticipated diversity. In terms of gaps we had no participation from specialists in the Orthoptera or Hemiptera. In the second of these cases this was a serious deficiency which we are attempting to address. Other notable omissions were treatments of Psocoptera and aquatic groups: both diverse from place to place within this rainforest. Of course our general sampling regime did sample these and other groups and samples are stored for future analysis.

Ecologically the project managed to cover most major functional groups: herbivores, detritivores and free-living predators. The parasitoids remain perhaps the most significant deficit in our analyses if one takes such a functional viewpoint. Once again the material is there.

So what can one conclude from such a retrospective? Basically in developing any comparative approach to forest diversity, either to test fundamental questions or to provide management tools, we will be limited by available taxonomic expertise. One of the most pleasing aspects of the IBISCA-Queensland project to date, has been the emergence of a group of keen postgraduate students who are 'picking up' particular taxa and developing their own expertise and enthusiasm for future studies using these groups as tools.

The Latitudinal Context

The results available to date, from virtually all taxa that have been adequately analysed, there appears to be high, mid- and low-altitude specialists. Under even relatively mild climate-change scenarios some of these species will become of conservation concern. The management responses that may be needed to address these concerns will vary depending on whether the risk incurred is local or global. In a few instances – such as the dung-beetles – we already know sufficient about the wider distribution of the species concerned to judge just how serious this conservation concern should be. In almost all other cases, however, our knowledge of the wider distribution of taxa is either unknown or uncollated. In order to inform this question we need comparative studies on rainforest locations at different latitudes within Australasia. The basis for such studies already exists in some latitudes. Sets of sites are already established in far north Queensland and in New Guinea (S. Williams, V. Novotny pers. comm.). Other obvious locations for comparative transects are the Eungella massif, the Dorrigo/New England region of northern NSW and the Barrington Tops region of central NSW. The foci of survey work on such additional transects can now be informed by the results of the IBISCA-Queensland transect and can be more focussed and selective than was appropriate in the Lamington case. Research on Lepidoptera, Formicidae, Collembola and Coleoptera on some of these proposed transects has begun.

ACKNOWLEDGMENTS

A project such as IBISCA-Queensland cannot function without major funding. We are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Global Canopy Programme, NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. We also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We are grateful to all these sources without which the project would not have been possible. In addition a very wide range of organisations and persons assisted in the realisation of the project. O'Reilly's Rainforest Resort and the Mt Cainbable Cabins provided accommodation and sustenance. Over 50 volunteers provided vital people power in the field and laboratory. The paper, particularly our discussion of atmo-

spheric dynamics and temeprature lape rates, has been much improved following the comments of Dr Clyde Wild who refereed the submission. Any errors, of course, remain ours alone.

LITERATURE CITED

American Meteorological Society. 2000. *Glossary of Meteorology*, 2nd edn. (American Meteorological Society, Boston).

Andrew, N.R. & Hughes, L. 2005. Arthropod community structure along a latitudinal gradient: implications for future impacts of climate change. *Austral Ecology* 30: 281-297.

Ashton, L.A., Kitching, R.L., Maunsell, S.C., Bito, D. & Putland, D.A. 2011. Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest - exploring indicators of climate change. *Memoirs of the Queensland Museum-Nature* 55(2): 375-389.

Baehr, B.C. 2011. Australian goblin spiders of the genus *Opopaea* (Araneae: Oonopidae). The species of the IBISCA-Queensland Project at Lamington National Park. *Memoirs of the Queensland Museum-Nature* 55(2): 413-437.

Baehr, B.C., Raven, R.J. & Hebron, W. 2011. Orsolobidae (Araneae) of the IBISCA-Queensland Project at Lamington National Park, Australia. *Memoirs of the Queensland Museum-Nature* 55(2): 439-449.

Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds) 2003. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. (Cambridge University Press, Cambridge).

Basset, Y., Corbara, B., Barrios, H., Cuenoud, P., Leponce, M., Aberlenc, H-P., Bail, J., Bito, D., Bridle, J.R., Castano-Meneses, G., Cizek, L., Cornejo, A., Curletti, G., Belabie, J.H.C., Dejean, A., Didham, R.K., Dufrene, M., Fagan, L.L., Floren, A., Frame, D.M., Halle, F., Hardy, O.J., Hernandez, A., Kitching, R.L., Lewinsohn, T.M., Lewis, O.T., Manumbor, E., Medianero, E., Missa, O., Mitchell, A.W., Mogia, M., Novotny, V., Odegaard, F., Oliviera, E.G., Orivel., J., Ozanne, C., Pascal, O., Pinzon, S., Rapp, M., Ribeiro, S., Roisin, Y., Roslin, T., Roubik, D.W., Samaniego, M., Schmidl, J., Sorensen, L.L., Tischeshkin, A., Van Osselaer, C. & Winchester, N.N. 2007. IBISCA-Panama, a large-scale study of arthropod beta diversity and vertical stratification in a lowland rainforest: rationale, study sites and field protocols. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique-Entomologie* 77: 39-69.

Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds) 2008. *Gradients in a Tropical Mountain Ecosystem of Ecuador*. (Springer, Berlin).

Beck, J. & Chey, V.K. 2008. Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. *Journal of Biogeography*. 35: 1452-1464.

Bito, D., Novotny, V., Burwell, C.J., Nakamura, A. Kitching, R.L. & Ødegaard, F. 2011. Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient. *Memoirs of the Queensland Museum-Nature* 55(2): 451-461.

Botes, A.M., McGeoch, M.A., Robertson, H.G., Niekerk, A. & Davids, H. 2006. Ants, altitude and change in the Northern Cape floristic region. *Journal of Biogeography* 33: 71-90.

Boulter, S.L., McDonald, W.J.F, Kitching, R.L., Zlucki, J.M. & Jessup, L.W. 2011. Plant reproductive phenology and the floral resources of an Australian subtropical rainforest. *Memoirs of the Queensland Museum-Nature* 55(2): 463-479.

Boulter, S.L., Lambkin, C.L. & Starick, N.T. 2011. Assessing the abundance of seven major arthropod groups along an altitudinal gradient in subtropical rainforest. *Memoirs of the Queensland Museum-Nature* 55(2): 303-313.

Bravo, D.N., Araujo, M.B., Romdal, T. & Rahbek, C. 2008. Scale effects and human impacts on the elevational species richness gradients. *Nature* 453: 216-220.

Burbidge, N.T. 1960. The phytogeography of the Australian region. *Australian Journal of Botany* 8: 75-211.

Burwell, C.J. & Nakamura, A. 2009. Ants with altitude: the potential of ants as climate change bioindicators in subtropical rainforest. *News Bulletin of the Entomological Society of Queensland* 37: 130-138.

2011. Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum-Nature* 55(2): 391-411.

Department of Environment and Heritage. 2004. *Threatened Species and Threatened Ecological Communities*. (Department of Environment and Heritage, Canberra).

Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible, asymmetrical approach. *Ecological Monographs* 67: 345-366.

Floyd, A.G. 1990. *Australian Rainforests in New South Wales*. 2 Volumes. (Surrey Beatty & Sons, Sydney).

Foster, P. 2001. The potential negative impacts of global climate change in tropical montane cloud forests. *Earth Science Reviews* 55: 73-106.

Fowler, D., Cape, J.N., Leith, I.D., Choularton, T.W., Gay, M.J. & Jones, A. 1988. The influence of altitude on rainfall composition at Great Dun Fell. *Atmospheric Environment* 22: 1355-1362.

Gagne, W.C. 1979. Canopy associated arthropods in *Acacia koa* and *Metrosideros* tree communties along an altitudinal transect on Hawaii Island. *Pacific Insects* 21: 56-82.

Gaston, K. 2008. Biodiversity and extinction: the importance of being common. *Progress in Physical Geography* 32: 73-79.

Greenslade, P., & Kitching, R.L. 2011. Potential effects of climatic warming on the distribution of Collembola along an altitudinal transect in Lamington National Park, Queensland. *Memoirs of the Queensland Museum-Nature* 55(2): 333-347.

Hebert, P.D.N. 1980. Moth communities in montane Papua New Guinea. *Journal of Animal Ecology* 49: 593-602.

Henry, A.J. 1919. Increase of precipitation with altitude. *Monthly Weather Review* 47: 33-41.

Hodkinson, I.D. 2005. Terrestrial insects along elevational gradients: species and community responses to altitude. *Biological Reviews* 80: 489-513.

Hopkins. M.S. 1975. *Species Patterns in the Subtroipcal Rainforest*, PhD Thesis. (University of Queensland, St Lucia, Queensland).

Hutley, L. (ed.) 2006. *A Guide to Lamington National Park*. (Envirobooks, Brisbane).

Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences* 97: 1630-1633.

Jacobson, M.Z. 2005. *Fundamentals of Atmospheric Modelling*. (Cambridge University Press, Cambridge).

Joint ANZECC/MCFFA National Forest Policy Statement Implementation Sub-committee, Technical Working Group. 1995. Broad Criteria for the Establishment of a Comprehensive, Adequate and Representative Forest Reserve System. Draft Report. (Government Printer, Canberra).

Kitching, R.L. 1994. Biodiversity and taxonomy: impediment or opportunity. Pp.253-268. *In*, C. Moritz, C. & Kikkawa, J. (eds), *Conservation Biology in Australasia and Oceania*. (Surrey Beatty, Sydney).

Kitching, R.L., Li, D.Q. & Stork, N.E. 2001. Assessing biodiversity 'sampling packages': how similar are arthropod assemblages in different tropical rainforests? *Biodiversity and Conservation* 10: 793-813.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology* 37: 284-297.

Kitching, R.L., Boulter, S.L., Vickerman, G., Laidlaw, M., Hurley, K.L. & Grimbacher, P.L. 2005. *The Comparative Assessment of Arthropod and Tree Biodiversity in Old-World Rainforests: The Rainforest CRC/Earthwatch Protocol Manual*. 2nd Edition Revised. (Rainforest CRC, Cairns).

Kitching, R.L., Braithwaite, R. & Cavanaugh, J. (eds) 2010. *Remnants of Gondwana: a Natural and Social History of the Gondwana Rainforests of Australia*. (Surrey Beatty, Sydney).

Laidlaw, M.J. 2009. PhD Thesis, University of Queensland, St. Lucia, Brisbane.

Laidlaw, M.J., McDonald, W.J.F., Hunter, J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradsect. *Memoirs of the Queensland Museum-Nature* 55(2): 271-290.

Lambkin, C.L., Boulter, S.L., Starick, N.T., Cantrell, B.K., Bickel, D.J., Wright, S.G., Power, N., Schutze, M.K., Turco, F., Nakamura, A. & Burwell, C.J. 2011. Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an Australian subtropical rainforest: one hundred thousand and counting! *Memoirs of the Queensland Museum-Nature* 55(2): 315-331.

Lawton, R.O., Nair, U.S., Pielke, R.A. & Welch, R.M. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* 294: 584-587.

Lookingbill, T.R. & Urban, D.L. 2003. Spatial estimation of air temperature differences from landscape-scale studies in montane ecosystems. *Agricultural and Forest Meteorology* 114: 141-151.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84: 137-152.

McDonald, W.J.F. & Thomas, M.B. 1990. *The Flora of Lamington National Park: a Preliminary Checklist of the Vascular Plant Species*. 2nd edn. (Deptment of Primary Industries, Queensland Government, Brisbane).

Ødegaard, F. & Diserud, O.H. 2011. Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park (Queensland, Australia). *Memoirs of the Queensland Museum-Nature* **55**(2): 359-374.

Olsen, M. & Lamb, D. 1988. Recovery of subtropical forest following storm damage. *Proceedings of the Ecological Society of Australia* **15**: 297-301.

Pepin, N. 2001. Lapse rate changes in northern England. *Theoretical and Applied Climatology* **68**: 1-16.

Pounds J.A., Fogden, M.P. & Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* **72**: 611-615.

Progar, R.A. & Schowalter, T.D. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas Fir, *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. *Ecography* **25**: 129-138.

Ribeiro, S.P. & Barbosa, M. daS. 2011. Gall densities and leaf-chewing damage distribution in an Australian subtropical forest. *Memoirs of the Queensland Museum-Nature* **55**(2): 481-493.

Schultze, C.H., Linsenmair, K.E. & Fiedler, K. 2001. Understorey versus canopy: patterns of vertical stratification among Lepidoptera in a Bornean rain forest. *Plant Ecology* **153**: 133-152.

Shoo, L.P., Williams, S.E. & Hero, J-M. 2006. Detecting climate change induced range shifts: where and how should we be looking? *Austral Ecology* **31**: 22-29.

Speight, M.R., Hunter, M.D. & Watt, A.D. 1999. *Ecology of Insects: Concepts and Applications*. (Blackwell Publishing, Oxford).

Staunton, K.M., Fellows, C.S., Kitching, R.L., Nakamura, A., Burwell, C.J. & Raven, R.J. 2011. Limited surrogacy between predatory arthropods along an altitudinal gradient in subtropical rainforest. *Memoirs of the Queensland Museum-Nature* **55**(2): 291-302.

Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R.L., Lindenmayer, D., Musgrave, W., Stafford Smith, M. & Werner, P. 2009. *Australia's Biodiversity and Climate Change: A Strategic Assessment of the Vulnerability of Australia's Biodiversity to Climate Change*. (CSIRO Publishing).

Still, C.J., Foster, P.N. & Schneider, S.H. 1999. Simulating the effect of climate change on tropical montane cloud forests. *Nature* **398**: 608-611.

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforests of Lamington National Park, Southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Tardieu, V. & Barneoud, L., 2007. *Santo: Les Explorateurs de Ile Planete*. (Belin, Paris).

Tree, D.J. & Mound, L.A. 2011 Thysanoptera of Lamington National Park, Australia, collected during the IBISCA-Queensland Project. *Memoirs of the Queensland Museum – Nature*. **55**(2): 349-358.

Westoby, M. & Burgman, M. 2006. Climate change as a threatening process. *Austral Ecology* **31**: 549-550.

Williams, S.E., Bolitho, E.E. & Fox, S. 2003. Climate change in Australian tropical rainforest: an impending environmental catastrophe. *Proceedings of the Royal Society of London* **270**: 1887-1892.

The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland.

Craig L. STRONG[1]

Sarah L. BOULTER[2]

Melinda J. LAIDLAW[3]

Sarah C. MAUNSELL[2]

David PUTLAND[4]

Roger L. KITCHING[2]

1. Atmospheric Environment Research Centre, Griffith School of Environment, Griffith University, Nathan Qld 4111 Australia; 2. Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: s.boulter@griffith.edu.au; 3. Queensland Herbarium, Biodiversity and Ecosystem Sciences, Department of Environment and Resource Management, Toowong Qld 4066, Australia. 4. Growcom, PO Box 202 Fortitude Valley Qld 4006, Australia

Citation: Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D. and Kitching, R.L. 2011 12 20: The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum – Nature* 55(2): 251-270. Brisbane. ISSN 0079-8835.

ABSTRACT

Climate and soil properties are key factors influencing vegetation and biota. As such, an understanding of the variability in climate and soil properties along an altitudinal gradient can be used to explain changes in vegetation and biota along the same gradient. Understanding these patterns can offer a powerful predictive tool with respect to changes in climate. The temperature, relative humidity and wind speed and direction were logged throughout the day and night for up to 333 days continuously at five different altitudes in the subtropical rainforest of Lamington National Park, Queensland, Australia. In addition, soil sampling was carried out at the same sites and elements of the physical, chemical and mineralogical characteristics of the soil tested. Temperature decreased with increased altitude, although less temperature variability was experienced at higher altitudes. All sites experienced relative humidity close to 100% for most nights throughout the year, although daily temperature increases reduced humidity at most sites. Increasing windiness at the highest (1100 m above sea level (a.s.l.)) altitude reflected meso-scale synoptic conditions. Soils demonstrated increasing moisture, organic matter and acidity as elevation increased. The macro- and micro-nutrients measured showed variable responses with nitrogen increasing and the other macro-nutrients decreasing with altitude. Aluminium increased exponentially with altitude. Moisture and temperature appear to be important drivers in soil parameters and therefore biological patterning along the transect. Future climate change resulting in atmospheric warming and drying are predicted to have a significant impact on moisture availability both in the canopy and soil environments. ❐ *altitudinal gradient, subtropical rainforest, microclimate, soils.*

Many insect and plant species are distributed along an altitudinal gradient, partially reflecting the changes in local climate. The main changes

observed in local climate along an altitudinal gradient involve changes in temperature, precipitation, humidity, wind speed and radiation (Barry 1992). The study of an altitudinal gradient therefore offers an alternative to experimentation when investigating long-term climate change (e.g. Williams *et al.* 2003, Hodkinson 2005, Chen *et al.* 2009). The predictable changes in abiotic conditions offer an opportunity to detect associated biotic patterns and, when matched with the predicted changes in physical parameters associated with climate change, offer a powerful predictive tool.

IBISCA, an international research programme, aims at studying the spatial (horizontal, vertical, altitudinal) and temporal distribution of arthropods and their interactions with plants and other selected organisms. The IBISCA-Queensland Project (Kitching *et al.* 2011) specifically explored the diversity of arthropods, plants and fungi from the soil to the rainforest canopy along an altitudinal transect in Lamington National Park, Australia, for the purpose of assessing and predicting the impact of climate change on biodiversity. Predicting biological changes along an altitudinal gradient also requires study of the edaphic conditions, as individual sites will experience considerable variability as a result of the interaction between topography, slope, aspect and meso-scale synoptic conditions (Proctor *et al.* 2007, Bendix *et al.* 2008, Wilcke *et al.* 2008, Gerold *et al.* 2008). In order to better quantify the climatic and physical changes associated with the different IBISCA-Queensland plots and altitudes, a programme of micrometeorological monitoring and a simple soil sampling scheme were devised. The aim of this paper is to describe the micrometeorological properties and soil characteristics associated with an 800 metre altitudinal gradient at Lamington National Park, Queensland, Australia. These findings provide an abiotic context to other IBISCA-Queensland research projects so that they may assess and predict the patterns of their focus taxa along the altitudinal gradient.

MATERIALS AND METHODS

Study site. The IBISCA-Queensland Project was conducted in the subtropical rainforest of Lamington National Park (28° 13′ S 153° 08′E). The project established 20 permanent plots, across five broad altitudes; 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). Each altitude had four replicated plots (A–D) spaced a minimum of 400 m apart. Plot selection was determined according to a hierarchy:

1. appropriate altitude;
2. all plots had to be within the same water catchment, West Canungra Creek; and
3. all plots had to be accessible to researchers carrying equipment on foot.

All plots had a 20 m x 20 m quadrant pegged out and a centrally positioned permanent metal post. This quadrant was the location for all baseline sampling for vegetation and arthropods (see Kitching *et al.* 2011). In addition, some projects also conducted sampling within a 50 m radius of the central metal post. A full description of the project rationale and scope are discussed in Kitching *et al.* (2011).

Geology and climate. Lamington National Park is located on the McPherson Range and associated spurs that form the northern flanks of the Mt Warning erosion caldera. The caldera is the largest and best preserved basaltic shield volcano in Australia (Willmott 2004) and is all that remains of a broad shield volcano which erupted between 24 and 20 million years ago (Graham 2001). Being on the northern section of the caldera, the study sites are dominated by rocks of the Tertiary Lamington Volcanics (Morand 1996). Three major periods of volcanic activity over a four million year lifespan have resulted in a complex banded geology. Beechmont Basalt is overlain by Binna Burra Rhyolite and scattered pyroclastic vents, and capped by younger Hobwee Basalt (Stevens 1976). Basalts in the region vary from fine-grained to textured dolerites and porphyritic

basalts and can be vasicular, scoriaceus or amygdaloidal (Morand 1996).

The subtle differences in basalt chemical composition, differential weathering characters and age of weathering surfaces, in conjunction with varied topography and the resulting microclimate has resulted in a wide variety of soil types (Beckmann & Thompson 1976). Contemporary erosional processes continue today, exposing fresh surfaces and depositing fresh alluvium. The alluvium is high in basalt derived clay and contains the products of both recent and historic weathering (Beckmann & Thompson 1976). Across the caldera, basalts on the plateaus generally weather to krasnozem soils while those on the slopes can form poorer lithosols (Beckmann & Thompson 1976).

Climate in the study region is driven by the movement of high and low pressure systems from the west, producing strong seasonal patterns (McDonald & Whiteman 1979). A pronounced wet season occurs during the austral summer driven by low pressure systems and tropical cyclonic depressions (Morand 1996). Almost thirty percent of annual precipitation falls between February and March while only seven percent is received between August and September. Moisture laden onshore winds are orographically lifted as they meet the McPherson Range, producing highly erosional rainfall particularly at the highest elevations. Rainfall is supplemented at higher elevations by low cloud and fog (Morand 1996). Evapotranspiration rates at Murwillumbah, located on the coastal side of the caldera, peak in December (5.3 mm/day) and are at a minimum in June/July (1.7 mm/day) (Morand 1996). The dry season, from winter to spring, is characterised by dry, westerly winds associated with the passage of cold fronts and by calm conditions associated with large stable high pressure systems (McDonald & Whiteman 1979). Under calm conditions frosts are common but their frequency and intensity is greatly affected by topography (McDonald & Whiteman 1979). The mountainous terrain produces innumerable microclimates linked with both coarse and fine scale changes in altitude, aspect and slope.

Microclimate. An automatic weather station (La Crosse WS-3600 Weather Pro, La Crosse Technology Ltd, USA.) was installed at each altitude. The station was positioned on the perimeter of the permanent 20 m x 20 m quadrats at sites 300D, 500A, 700A, 900A, 1100B. Weather parameters measured included temperature, relative humidity, rainfall, atmospheric pressure, dewpoint temperature, wind speed and wind direction. All parameters were measured at a height of 1.5 m a.s.l., except rainfall which was measured at ground level. The weather stations recorded data every thirty minutes from October 2006 until February 2008. However, the fine electronics of the tipping bucket rain gauge failed to operate at all sites due to high moisture conditions and insect activity associated with the forest floor. Instead, rainfall data was derived from two Bureau of Meteorology rainfall stations. At an altitude of 100 m, the Finch Road Canungra station (BoM Station Number 40042; 28.01°S, 153.17°E) is located 17 km downstream from the 300 m altitude plots and operated from 1916 to 2008. At an altitude of 917 m, the Green Mountains station (BoM Station number 40182; 28.23°S, 153.14°E) is located in very close proximity to the 900 m plots and has operated from 1916 to the present. The long-term rainfall record (greater than 90 years) at the two altitudes (900 m and 300 m), whilst not providing data from the IBISCA plots, does give an overview of the differences between altitudes.

A temperature and humidity data logger (LogTag ™ HAXO-8, LogTag Recorders Ltd., Auckland, New Zealand) was installed at both the understorey and canopy levels on each of the 20 plots to increase the spatial monitoring of these important parameters. The data loggers recorded temperature and humidity every 60 minutes with a memory capacity of 333 days. Loggers in the understorey were attached to the centre post of each plot at 1.5

m a.s.l. and sampled between July 2007 and mid June 2008. Loggers in the canopy were suspended in the upper (but not outermost) canopy, as close as possible to directly above the centre post. Installation of the canopy loggers was more difficult and therefore occurred over a two week period from late September to early October 2007 with the units running for 333 days up until early October 2008. As the height of the canopy varied between altitudes (35 m at 300 m a.s.l. and 25 m at 1100 m a.s.l.) the height of the loggers also varied, but importantly the measurements represented the local canopy microclimate. They were installed without any environmental enclosure (e.g. Stevenson screen) affecting, at times, the quality of data. For example, occasional canopy temperatures at one plot will be 10 degrees higher than any other plot at the same altitude at the same time. We assumed that this resulted from direct exposure to the sun and have excluded any such outliers in our analyses.

Soil. A single set of soil samples was collected from each of the 20 plots between March 11-14, 2008. Sampling occurred two weeks after widespread regional rainfall. Five samples were taken randomly within each plot by first scraping aside all leaf litter and surface organic matter and obtaining a 6 cm by 6 cm by 15 cm deep core. The five cores from a plot were then thoroughly mixed and a sub-sample extracted to represent each plot. A range of soil chemical analyses were carried out by Phosyn Analytical Pty Ltd (Andrews, Queensland) with all extraction protocols following those outlined in Rayment and Higginson (1992). Soil pH was analysed potentiometrically, in both 0.01 M $CaCl_2$ and water, using a soil-dilutant ratio of 1:5. Organic matter percentage was determined from loss on ignition (360°C for 2 hours). Cation exchange capacity (CEC) was derived by calculation. Electrical conductivity (EC) was analysed potentiometrically via a soil-water ratio of 1:5. Ammonium (NH_4^+-N) and nitrate (NO_3^--N) were extracted with water and analysed with segmented flow analysis. Trace elements sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) were extracted with ammonium acetate and analysed with inductively coupled plasma atomic emission spectrometry (ICPAES). Copper (Cu), zinc (Zn), manganese (Mn) and iron (Fe) were extracted with diethylenetriaminepentaacetic acid (DTPA) and analysed using inductively coupled plasma atomic emission spectrometry (ICPAES). Aluminium (Al) was extracted with potassium chloride (KCl), sulphur(S) in MCP and chloride (Cl) in water. All were analysed with ICPAES. Phosphorus (P) was analysed following the Olsen-extraction technique determination via spectroscopy. A low resolution texture analysis was conducted by hand texturing and colour was determined using Munsell colour notation on dry samples.

Additional temporal measurements of soil moisture were made by one of us (SM) at three of the altitudes 700, 900 and 1100 m a.s.l.. Sampling was undertaken every two to three months between August 2008 and April 2009 at all four plots at each of the three altitudes. Sampling across the altitudes occurred in a two to three day period with the exception of the 700D sample in October 2008 which could not be accessed for ten days due to logistical problems and therefore this sample was excluded from analysis. Five sub-samples of soil were taken from each plot on each sampling occasion. Leaf litter was first removed and then twenty-five to thirty grams of soil (to 8 cm deep) was collected with a trowel and transferred to pre-weighed soil moisture tins. The percentage of moisture in each sub-sample of soil was measured using the gravimetric method (Rayment & Higginson 1992) and then averaged across the five sub-samples.

The means of all soil parameters (except texture and soil colour) were compared across altitudes using one-way ANOVA. A two-way repeated-measures ANOVA was used to test for differences in temporal soil moisture data; the two independent variables in the model

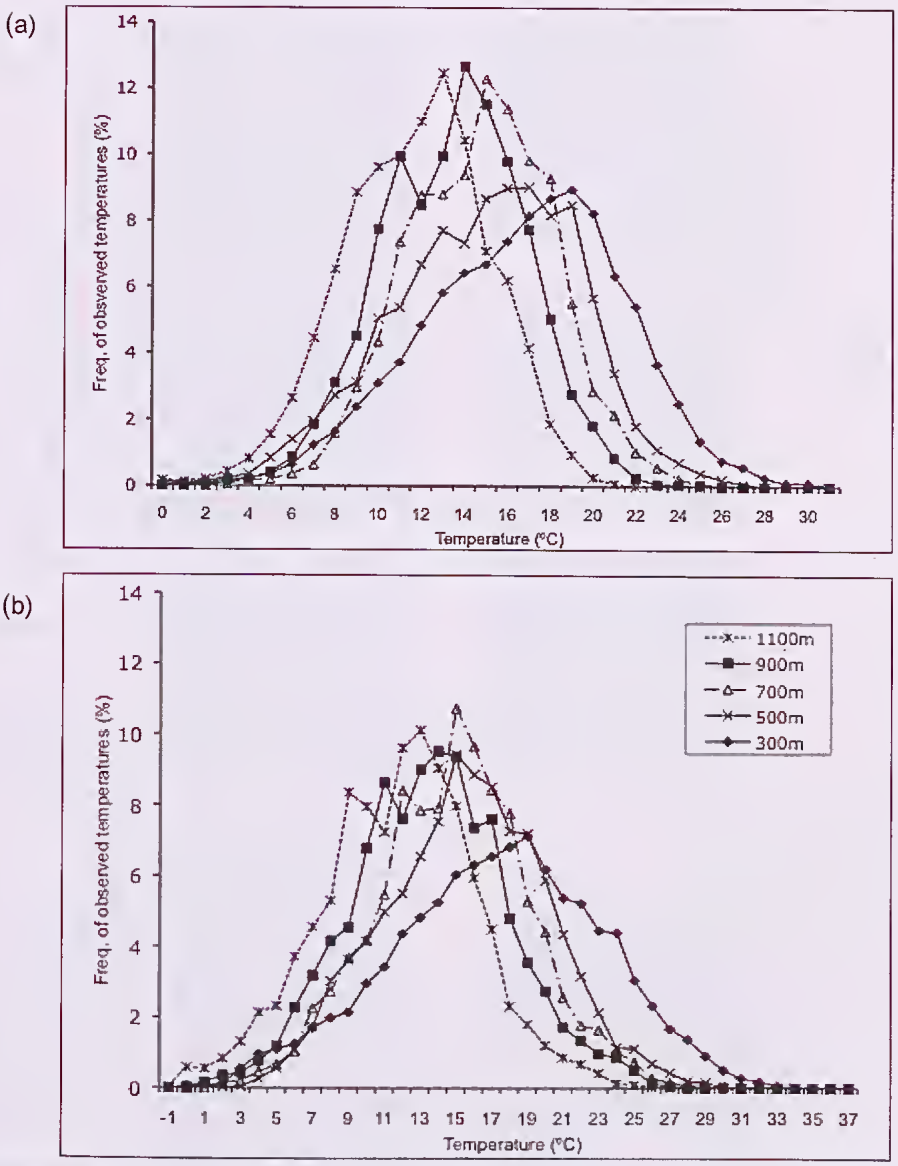


FIG. 1. Frequency (percent) of temperatures averaged across four plots at each of five altitudes in the rainforest, a) canopy and; b) understorey of Lamington National Park. Temperatures were recorded hourly across 333 days for each plot, across a range of dates from July 2007 to June 2008.

being time of year (month) and altitude. This more detailed statistical analysis of soil moisture acknowledges that measurements taken repeatedly through time on the same plots, could lead to the expectation that measurements taken closer together in time are more highly correlated than measurements taken further apart.

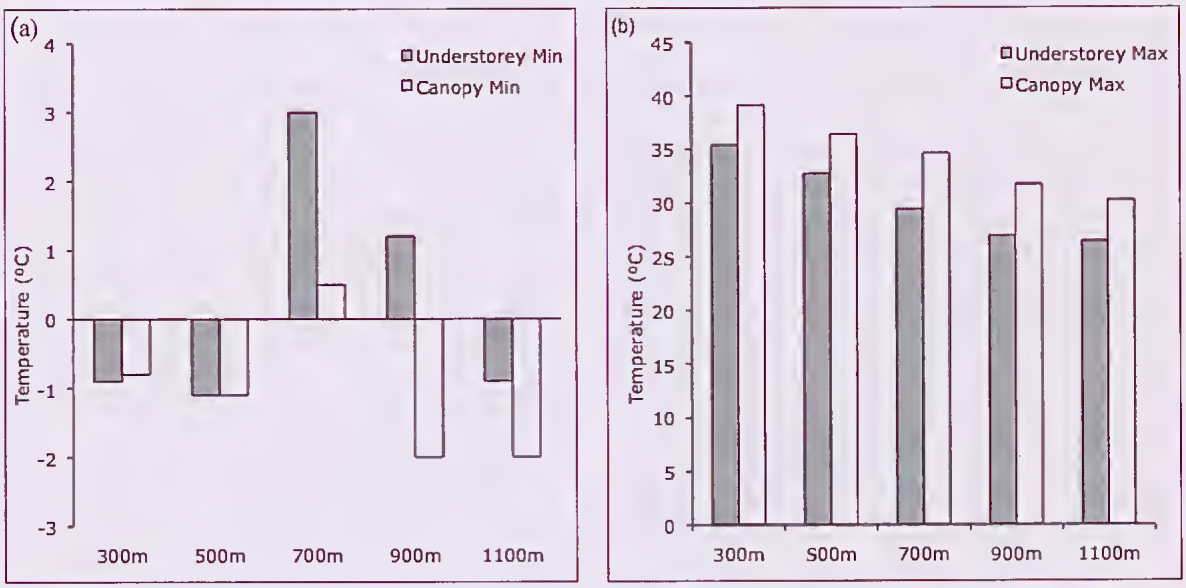


FIG. 2. Absolute (a) minimum temperatures and (b) maximum temperatures recorded in both the canopy and understorey across five altitudes recorded from July 2007 until August 2008.

RESULTS

Microclimate. The following results represent the first attempt at characterising micro-meteorological variations between small altitudinal increments of 200 metres at Lamington National Park. They provide general trends for temperature, relative humidity, wind speed and direction. Unfortunately, gaps in the data existed at all sites. Of the five weather stations, the 300 m had the most incomplete record with only 53% of observations successfully recorded. This particular location had access difficulties due to flooding and property management, prohibiting regular downloading of data and battery changes. Of the other four weather stations 73% of the data was collected at the altitude of 500 m altitude, 61% at 700 m a.s.l., 63% at 900 m a.s.l. and 73% at 1100 m a.s.l.. Greater continuity of recording was achieved using the data loggers. Hourly readings of temperature and humidity were obtained for all LogTag data loggers at all plots with the exception of those in the canopy at two of the 1100 m a.s.l. plots. Both of these data loggers failed during the course of the 333 days of recording. Despite these limitations, the micro-meteorological results provide extremely useful insights into the abiotic drivers of ecological diversity.

Temperature. Both the median air temperature and the range in air temperatures decreased with increasing altitude. Expressed as frequency distributions, the median air temperature for both canopy and understorey become cooler as altitude increased (Fig. 1). Temperature differences (ΔT) between 300 m and 1100 m a.s.l. for both canopy and understorey were between 6 to 7°C, representing an average air temperature gradient (i.e. a decrease in temperature with increasing altitude) of 0.75 °C 100 m^{-1}. The range of temperatures experienced

FIG. 3. (Opposite page) Hourly temperature (°C) in the understorey (1.5 m above ground level) and canopy (25-35 m) of rainforest, averaged across four plots, at each of five altitudes along the IBISCA-Queensland gradient. Temperature was recorded by LogTag data loggers.

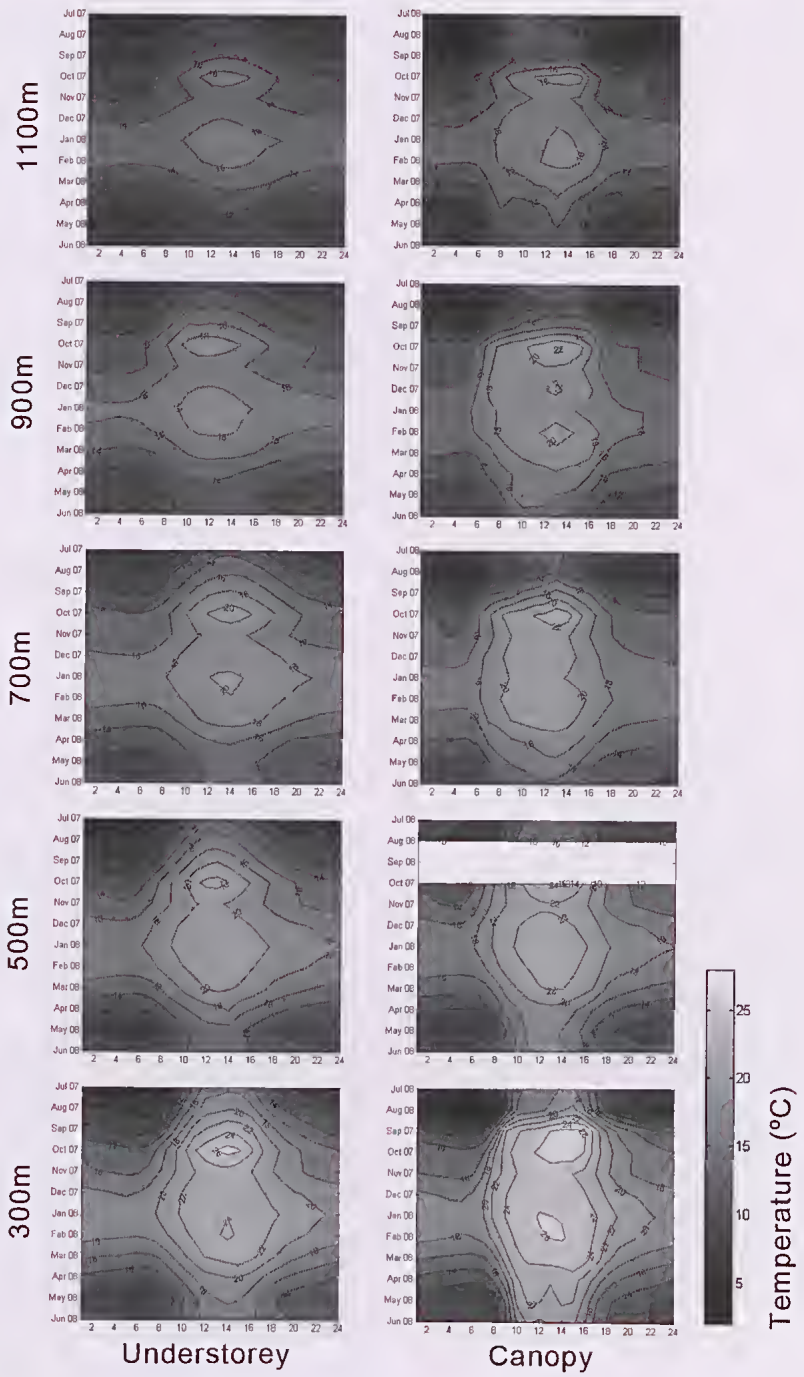

1100m
900m
700m
500m
300m
Understorey
Canopy
Time of day (24:00hrs)
Temperature (°C)
5
10
15
20
25

TABLE 1. Mean measurements of soil characteristics at each of five altitudes (four plots per altitude) along a gradient in Lamington National Park and their overall direction of change in relation to increasing altitude. S.E. in parenthesis after means. * indicates those variables that were significantly different between altitudes using one-way ANOVA, P<0.05. # indicates the trend was not strictly linear.

Soil Physical Parameter	Altitude					Direction of change with increased altitude
	300m	500m	700m	900m	1100m	
pH [H2O] *	6.4(0.14)	6(0.2)	5.425(0.39)	4.575(0.13)	4.325(0.06)	Decrease
pH [CaCl2] *	6.025(0.11)	5.625(0.17)	4.95(0.38)	4.15(0.12)	3.925(0.03)	Decrease
Organic Matter (%) *	12.05(1.01)	15.85(0.74)	14.95(0.75)	21.5(1.59)	27.175(2.23)	Increase
CEC (meq/100g) *	31.775(3.45)	29.65(2.19)	18.375(5.39)	7.975(0.94)	5.85(0.24)	Decrease
EC (dS/m)	0.1575(0.01)	0.165(0.01)	0.155(0.01)	0.125(0.01)	0.1275(0.004)	N/A
Ca base saturation (%) *	67.15(0.74)	70.95(4.67)	65.55(5.13)	46.3(10.58)	19.575(2.62)	Decrease
K base saturation (%) *	3.125(0.21)	2.475(0.09)	4.025(1.05)	5.75(0.29)	7.4(0.57)	Increase
Mg base saturation (%)	28.425(0.59)	25.125(4.23)	25.625(2.86)	22.5(4.06)	18.925(2.3)	N/A
Na base saturation (%) *	1.175(0.18)	1.2(0.34)	1.425(0.3)	2.4(0.16)	3.2(0.36)	Increase
Al base saturation (%) *	0.15(0.03)	0.25(0.03)	3.4(1.86)	23.075(14.04)	50.925(4.73)	Increase
Ca:Mg Ratio *	2.4(0.07)	3.15(0.66)	2.725(0.5)	1.975(0.26)	1.025(0.05)	Decrease #
Moisture (%) *	22.52(0.83)	26.24(0.98)	26.76(1.4)	33.55(1.81)	44.37(0.77)	Increase

at the 300 and 500 m a.s.l. plots were greater than those at the 700, 900 and 1100 m a.s.l. plots (Fig 1), with the 300 m a.s.l. plot experiencing a ΔT of up to 30°C (for the understorey) and a ΔT of 22°C at the highest altitude plot (Fig. 1).

The absolute maximum temperature also decreased with increasing altitude for both understorey and canopy level (Fig 2a). Absolute minimum temperatures, however, did not display a linear decrease, with the values at the two lowest altitudes less than those experienced at the 700 m a.s.l. sites. However, the absolute minimums were lower at the 1100 m a.s.l. compared to the 300 m a.s.l. plots (Fig. 2b). The canopy experienced colder minimums than the understorey for the three highest altitudes (i.e. 700, 900 and 1100 m a.s.l.) (Fig. 2b). Across the five altitudes, understorey temperatures experienced ΔT values of up to 3°C less than canopy (Fig. 2b) and the difference between the absolute maximum and minimum temperature decreased with increasing altitude.

Diurnal and seasonal fluctuations in temperature were, as expected, experienced at all altitudes and in both the canopy and understorey (Fig. 3) over the sampling periods. The greatest difference in air temperature between the altitudes was experienced during day light hours (Fig. 3).

Relative humidity. Relative humidity clearly increased with altitude for both the understorey and canopy (Fig. 4). Diurnal and seasonal

TABLE 2. Mean measurements of soil nutrients at each of five altitudes (four plots per altitude) along a gradient in Lamington National Park and their overall direction of change in relation to inceasing altitude. S.E. in parenthesis after means. * indicates those variables that were significantly different between altitudes using one-way ANOVA, $P<0.05$. # indicates the trend was not strictly linear.

Soil Nutrients – Macro	Altitude					Direction of change with increased altitude
	300m	500m	700m	900m	1100m	
Macro nutrients						
Nitrate (ppm) *	9(1.98)	9.175(1.28)	15.2(3.33)	12.35(1.99)	20.5(3.48)	Increase
Ammonium (ppm) *	4.5(0.73)	5.525(1.08)	7.175(0.93)	9.375(1.02)	13.95(1.76)	Increase
Phosphorus (ppm)	31.75(4.71)	23.5(4.63)	19(1.68)	21.5(3.23)	21.25(2.29)	N/A
Potassium (ppm) *	381.25(40.99)	284.25(12.35)	229(40.03)	177(18.47)	168(8.64)	Decrease
Calcium (ppm) *	4270.5(477.91)	4268.5(556.27)	2551(873.55)	788.5(221.71)	232(41.24)	Decrease
Magnesium (ppm) *	1093.75(124.24)	869.75(80.49)	540.25(142.04)	227.5(55.65)	135.5(22.38)	Decrease
Micro nutrients						
Sulphur (ppm) *	12.25(0.48)	14.5(1.04)	20.25(3.77)	28.25(1.55)	29.75(2.29)	Increase
Boron (ppm) *	1.925(0.17)	1.575(0.28)	2.05(0.39)	1.125(0.13)	0.675(0.05)	Decrease
Copper (ppm)	1.325(0.19)	1.4(0.19)	1.825(0.26)	1.6(0.14)	1.05(0.09)	N/A
Iron (ppm) *	52.75(2.95)	66.75(3.57)	52.75(5.3)	69.5(8.19)	89.5(8.39)	Increase
Manganese (ppm) *	67.925(9.48)	55(3.1)	105.25(17.16)	69.65(20.33)	21.15(5.57)	Decrease #
Zinc (ppm) *	6.1(0.75)	4.4(0.36)	11.25(2.95)	1.825(0.32)	1.225(0.2)	Decrease #
Aluminium (ppm) *	3.75(0.48)	6.5(0.5)	30.25(12.59)	135(65.44)	264.75(17.56)	Increase
Sodium (ppm)	81.75(2.75)	75.75(14.23)	55(19.34)	43.25(2.95)	43.25(5.71)	N/A
Chloride (ppm) *	17.75(1.93)	16.25(1.03)	16.25(1.8)	22(0.91)	32.25(3.33)	Increase #

fluctuations in relative humidity were observed for all altitudes in both the understorey and canopy using the data loggers (Fig. 4). Humidities were highest during summer daytime, particularly at 1100 m elevation where the moist daytime conditions continued over a longer time period than all other altitudes. Relative humidity was higher in the understorey than in the canopy (Fig. 4). Relative humidity measured by the automatic weather stations from December 2006 – December 2007 showed similar diurnal and seasonal patterns (Fig. 5) with prolonged moisture levels both day and night also seen at the 1100 m a.s.l. plot.

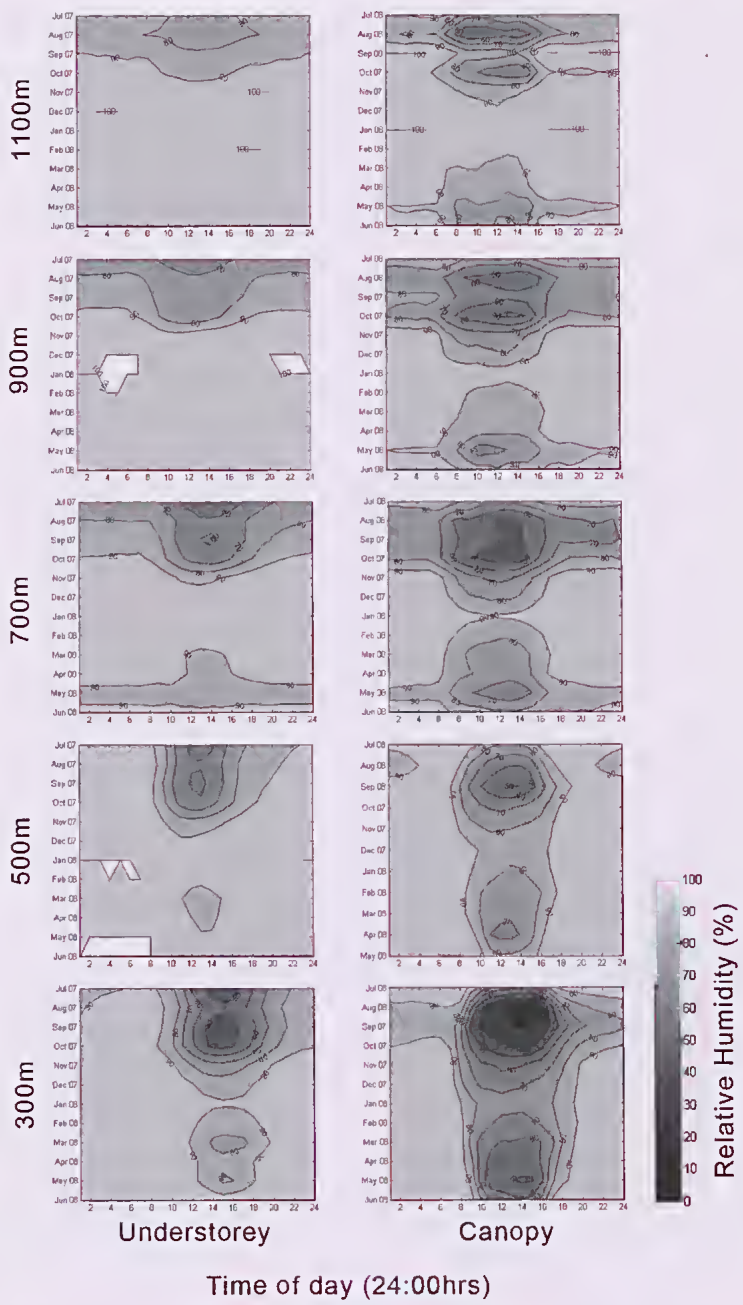


FIG. 4. Hourly relative humidity (%) in the understorey (1.5 m above ground level) and canopy (25-35 m) of rainforest, averaged across four plots, at each of five altitudes along the IBISCA-Queensland gradient. Relative humidity was recorded by LogTag data loggers.

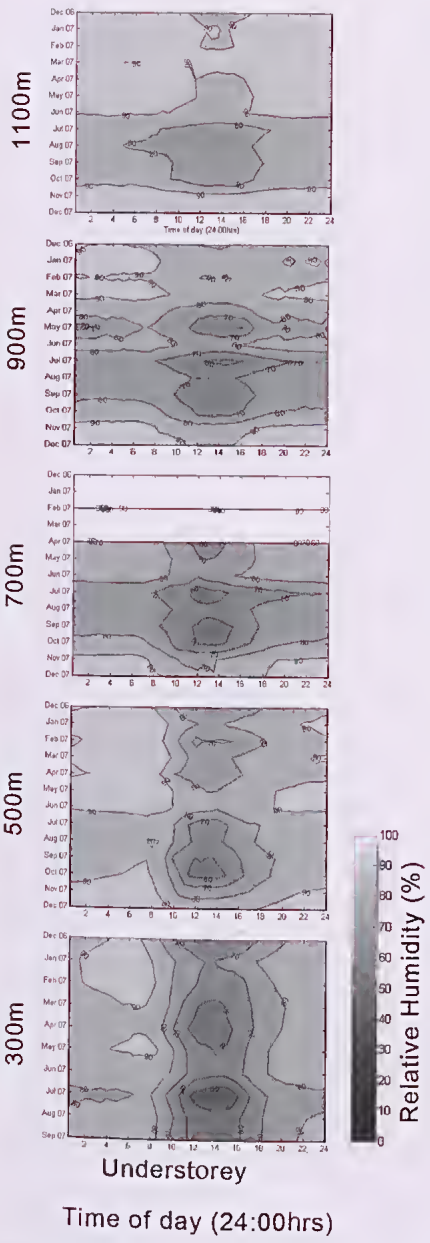


FIG. 5. Hourly relative humidity (%) measurements taken from five automatic weather stations, one at a plot within each of the five different altitudes, mounted approximately 1.5 m above ground level with readings averaged per month from December 2006 to December 2007.

Wind speed and direction. There was a clear increase in the incidence of wind with increasing altitude. Low altitude plots showed infrequent wind activity with wind speeds no more than gentle air movement (less than 2 m/s). In contrast, the 1100 m a.s.l. plot had frequent strong wind activity (greater than 12 m/s) (Fig. 6). Wind direction differed with altitude during the observation period with low altitudes experiencing predominantly north-easterly winds, clearly contrasting with the 1100 m a.s.l. plot where south-westerly winds prevailed.

Rainfall. Due to rainfall gauge failures, we consider here only the difference in rainfall at two altitudes – 900 m a.s.l. and 100 m a.s.l.- at Lamington National Park by utilising two long-term Bureau of Meteorology rainfall stations within the study catchment.

The long-term monthly rainfall averages over the past 92 years indicate the higher altitude rainfall location (917 m a.s.l.) receives on average, 21% more rainfall than the lower location (100 m a.s.l.), with the largest differences occurring in late summer and early winter (Fig. 7). Summer and early autumn is the dominant rainfall season, with late winter/early spring the driest at both altitudes. Comparing monthly totals between 2006 and 2008, we note that approximately 65% of monthly totals fell below the long-term average and that both within year and between year patterns between the two altitudes were generally similar, with the exception of extraordinarily higher rainfall totals at the 917 m weather station in January 2008 (Figs 8a, b).

Soil. Derived from Tertiary basaltic rocks, all plots had soils of loam to silty clay loam Krasnozem Gn4.11 or Gn4.12 in Northcote classification (Northcote 1979) and Ferralsol in FAO classification (FAO 1998). These Ferralsols have loamy textures with colours ranging from grey-browns at lower altitudes (300 and 500 m a.s.l.) and dark browns at the higher altitude plots (700, 900 and 1100 m a.s.l.). There were slight differences in topographic

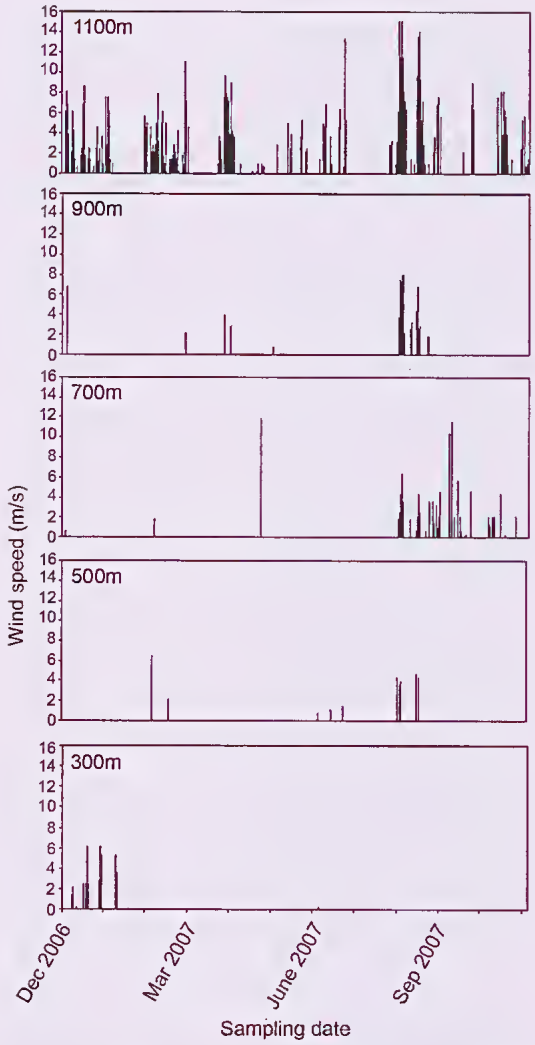


FIG. 6. Incidence of wind events at each of five altitudes between December 2007 and December 2007 as measured by automatic weather stations. Low altitude plots had infrequent, low wind speed events, while the 1100 m a.s.l. plot had stronger and more frequent events.

position between altitudes. The 300 m a.s.l. plots were positioned in the valley bottoms, partially on the flood plain of Canungra Creek. These plots had a southerly orientation and an average inclination of 10°. The 500 m a.s.l. plots were on the lower mid slopes in close proximity to the high intensity zone of Canungra Creek. Orientation was southerly, with the exception of plot 500A, which was north-easterly, and slope angles averaged 10°. Positioned on the mid and upper slope, the 700 and 900 m a.s.l. plots were distant from Canungra Creek, instead situated in the vicinity of small gullies producing the upper tributaries of the catchment. These plots had a north-easterly orientation and average inclinations of 12° and 17° respectively. The 1100 m a.s.l. plots were located along a north-west to north-east facing ridge-line and had the greatest variation in slope of between 5° and 25° (average 14°). As some soil properties are known to vary because of slope processes, slope position should be considered when interpreting the soil data. The analysis presented here evaluates altitudinal variation alone.

Altitudinal variation of soil chemical parameters and texture. The chemical and physical analysis of the soil samples collected at all altitudes showed changes in almost all parameters measured along the transect (Tables 1, 2). Overall, the soils in the research area were acidic, with pH ranging from 6.0 to 3.9 and decreasing with altitude (Table 1). There was a clear increase in soil organic matter within the A horizon soils associated with increasing altitude (Table 1). The percentage of organic matter at the highest altitude was almost one third of the total soil, while at the 300 m a.s.l. sites, the organic matter constituted a little over 10% of the soil. The proportion of soil moisture almost doubled between the 300 m (mean = 22.52%) and the 1100 m (mean = 44.37%) sites, with a steady increase along the altitudinal gradient (Table 1). The cation exchange capacity (CEC) of the soil decreased considerably with altitude. The CEC at the highest altitude was dominated by Al ions occupying 44% of the exchange capacity and the change in Al base saturation percent was exponential from the lowest altitude to the highest altitude (Fig. 9).

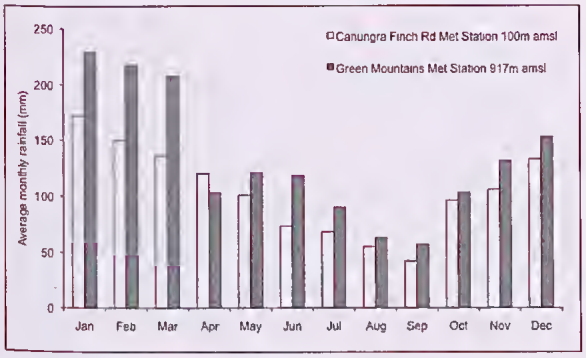
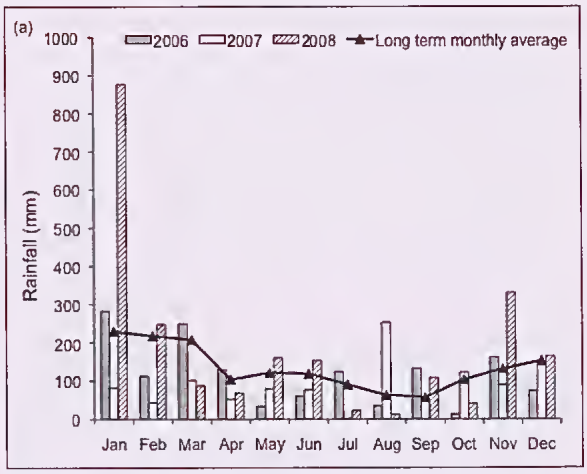


FIG. 7. Long-term monthly rainfall averages within and adjacent to Lamington National Park over the past 92 years at 917 m a.s.l. (Green Mountains Met station) and 100 m a.s.l. (Canungra Finch Road Met station). Source: Australian Bureau of Meteorology.

The macronutrients potassium, calcium and magnesium clearly decreased with altitude and showed a significant difference between altitudes (ANOVA, $P<0.05$) (Table 2). Phosphorous weakly decreased in concentration with increasing altitude but this trend was not significant. Calcium base saturation percent proportionally decreased with increasing altitude as aluminium saturation increased, with the 900 and 1100 m plots exhibiting distinct changes (Fig. 9). Of the macronutrients (N, P, K, Ca, Mg), nitrogen (measured as nitrate and ammonium) did not follow the general trend and increased with increasing altitude (Table 2).

The quantities of trace elements detected in the soil with increasing altitude varied. Sulphur, iron, aluminium and chloride increased with altitude and the differences between altitudes were significant (ANOVA, $P<0.05$) (Table 2). As altitude increased, there was a corresponding, significant decrease in the concentrations of boron, manganese and zinc (ANOVA, $P<0.05$), but no patterns were noted for copper and sodium (Table 2).

Soil moisture. Soil moisture, measured on five sampling occasions (months), consistently increased with increasing altitude (Fig. 10). A significant interaction, however, was found between altitude and the sampling month ($F = 4.83$, $P<0.001$) indicating that, although soil moisture increased with altitude at each month, the differences in soil moisture between each



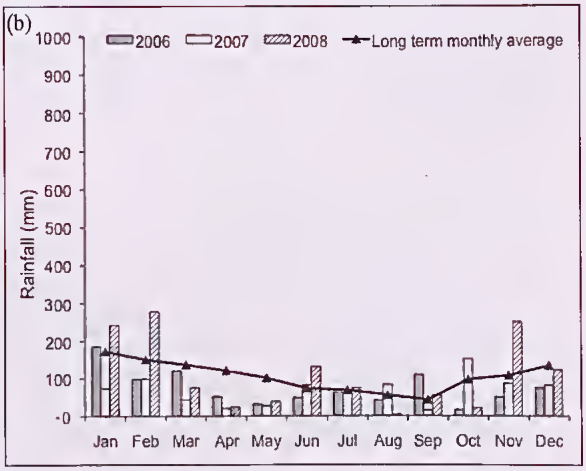


FIG. 8. Monthly rainfall totals collected in or adjacent to Lamington National Park at (a) 917 m a.s.l. (Green Mountains Met station) and (b) 100 m a.s.l. (Canungra Finch Road Met station) over the duration of the IBISCA-Queensland Project (2006-2008) compared with the long-term monthly averages for both sites (see Fig. 7). Approximately 65 % of the monthly totals fell below the long-term average yet rainfall at the two locations followed similar patterns. Data source: Australian Bureau of Meteorology.

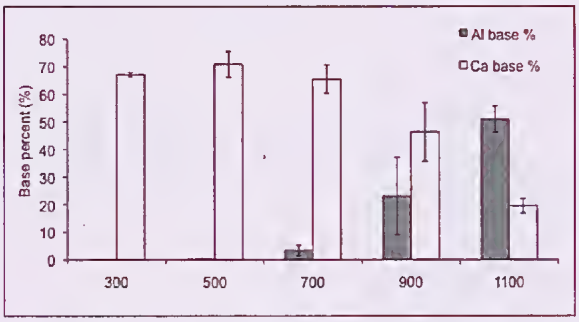


FIG. 9. The increase of aluminium ions in the A horizon from 300 to 1100 m a.s.l. compared to the decrease of calcium ions.

altitude group changed through time. This is apparent in Fig. 10 where it is clear that the 700 and 900 m a.s.l. altitudes tended to track each other through time, while the 1100 m a.s.l. plots experienced a more constant higher level of moisture (Fig. 10).

DISCUSSION

The climate data collected at the five altitudes along the IBISCA-Queensland transect are broadly consistent with previously described changes along altitudinal gradients elsewhere in the world (Bendix *et al.* 2008, Hutley *et al.* 1997, Hodkinson 2005) in demonstrating a general decrease in temperature, an increase in moisture levels and an increase in windiness. Likewise, trends in soil properties are similar to other published accounts of altitudinal gradients (Proctor *et al.* 2007) with decreasing pH and increasing organic matter and soil moisture with increasing altitude. This study has shown, however, that underlying these general trends are more complex climatic responses. These differences have potentially significant implications for the plant and animal communities that exist at different altitudes. Here we discuss the processes at work and the implications for ecosystem function and diversity.

Climate variability with increasing altitude. The average air temperature gradient of 0.75°C 100 m^{-1} along the IBISCA-Queensland transect is within the moist adiabatic lapse rate range (0.4 -0.8°C 100 m^{-1}) experienced along the eastern Australian seaboard (Sturman & Tapper 2006). Seasonal changes in environmental lapse rates were observed along the IBISCA-Queensland transect with peak austral summer (January) experiencing a moist adiabatic lapse rate of 0.75°C 100 m^{-1} compared to the drier austral winter (August) with a dry adiabatic lapse rate of 1.13°C for every 100 m increasing altitude. As a result, the 1100 m a.s.l. plots experienced colder winters, but effectively more stable temperature conditions than the lower altitudes that have cold overnight winter temperatures, but relatively warm days. Therefore, based on temperature range alone, it could be expected that the cooler but more stable temperature regimes at the 1100 m a.s.l. plots may benefit particular species thus producing a different suite of organisms compared to the 300 and 500 m a.s.l. plots.

The absolute minimum temperatures experienced at the different altitudes did not follow the expected trend of decreasing temperature with altitude (Hutley *et al.* 1997). The 300 and 500 m a.s.l. plots were colder compared to the higher altitudes (Fig. 2) potentially reflecting differences in topographic features between altitudes. Low sun angles in winter deliver the least amount of solar radiation to the Earth's surface (Sturman & Tapper 1996) and therefore southern slopes of escarpments such as both the 300 and 500 m a.s.l. IBISCA-Queensland plots, are most strongly impacted. This enhances colder minimum temperatures at the lower slopes. This is exacerbated by downward movement of air off the surrounding slopes converging to produce zones of cold air drainage (Sturman & Tapper 1996). The understorey at the higher altitude plots (i.e. 700, 900 and 1100 m a.s.l.) appeared to be unaffected by cold air drainage and had absolute minimum temperatures buffered by the canopy. Above 900 m a.s.l., canopy minimum temperatures reflected the average environmental lapse rate of 0.75 °C 100 m^{-1} by becoming colder than the absolute minimums experienced at the plots lowest in the valley.

Moisture is critical for the presence and survival of subtropical rainforests along Australia's east coast, particularly during July, August and September, when Lamington experiences a dry season (Fig. 7). Sources of moisture in rainforests, both tropical and subtropical, include precipitation, wind-blown (near horizontal) rain and cloud or fog droplets collecting on vegetation surfaces. Frequent cloud immersion and fog events are known to occur at altitudes of 800 to 900 m and above (Hutley *et al.* 1997). Hutley *et al.* (1997) determined that the moisture provided by fog deposition accounted for an additional 40% of rainfall collected at a subtropical rainforest site at 1000 m a.s.l. Stripping moisture from fog associated with high relative humidity results from the cool vegetation acting as a condensation surface. Vegetation, especially in the understorey (because insufficient solar radiation penetrates to warm leaves), produces ideal surfaces for the condensation of water vapour in the form of fog, thereby providing liquid water for biological processes. Low temperatures during winter increase relative humidity and lower dewpoint temperature (Sturman & Tapper 1996) increasing the likelihood of sourcing water from fog stripping (Richards 1996). At the higher altitudes above 900 m, the relative humidity climbed to at least 90% nightly during winter, except for a short time (one week) over mid-winter when relative humidity stayed around 60% (Fig. 4). Lower altitudes have a lower frequency of high relative humidities,

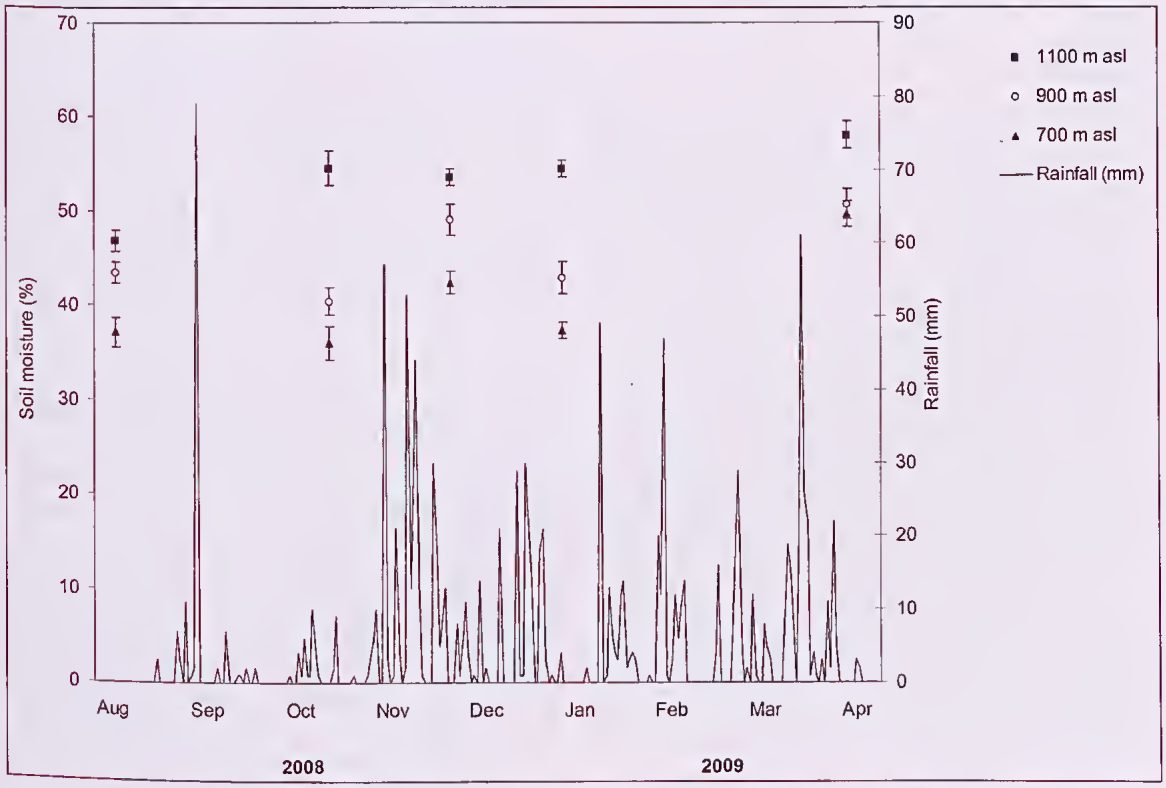


FIG. 10. Mean (± 1 S.E.) soil moisture (%), averaged across four replicate plots, for each of three altitudes (700, 900 and 1100 m a.s.l.) on five sampling occasions (months) at Lamington National Park and daily rainfall (mm), measured at 913 m a.s.l. (O'Reilly's Alert Station; number 40931) over the entire sampling period (source: Australian Bureau of Meteorology).

reducing the opportunity for fog stripping. Water inputs into the higher altitude sites will therefore be greater than those at lower altitudes, impacting on the distribution and composition of communities.

Rainfall totals were greatest at the higher altitude reflecting the effect of topography and meso-scale synoptic patterns. The long-term average annual rainfall measured at 917 m a.s.l. is 1590 mm compared to 1260 mm at an altitude of 100 m a.s.l. (Fig. 8). Topography drives much of this difference, as higher altitudes receive rainfall resulting from orographic uplift. Mountain ranges that face an onshore breeze force the moisture laden winds higher into the atmosphere, condensing the water vapour and often forming cloud and rain (Primack & Corlett 2005). Located on the northern section of the caldera, the higher altitude IBISCA-Queensland plots receive the regular south east trade winds that blow off the Pacific Ocean bringing the moisture associated with a maritime breeze (Sturman & Tapper 1996). This effect is apparent in January 2008 when the 917 m a.s.l. location received over three times as much rainfall as the low altitude location, potentially due to these strong onshore breezes (BoM 2008). In contrast, the two sites received similar rainfall totals in the following month (February 2008) when a meso-scale synoptic event brought widespread rainfall. During this event, an upper level trough moved eastward, combining with moisture laden onshore winds to produce widespread thunderstorms and heavy rain (BoM 2008). This impacted a large regional area whilst not discriminating for altitude.

Meso-scale synoptic events impact moisture delivery, humidity and evapotranspiration. During the drier months, cold fronts move across the country, often bringing strong dry winds (Reeder & Smith 1992) and a reduction in humidity. This results in higher vapour pressure deficits, the deficit between the amount of moisture in the air and how much moisture the air can hold when it is saturated, and the canopy at higher altitudes enduring high evapotranspiration stress. In contrast, the austral summer brings meso-scale low pressure systems from the southward annual migration of the Inter tropical Convergence Zone (ITCZ) (Sturman & Tapper 1996, Primack & Corlett 2005). This results in extended periods of near saturation at the highest altitudes and a strong tendency for cloud formation and water harvesting via cloud inception (Reeder & Smith 1992). While the lower altitudes are still impacted by meso-scale synoptic patterns, their microclimatic drivers such as local topography and proximity to water sources partially mitigate the full effect of meso-scale drivers (Primack & Corlett 2005).

Wind direction over the observation period changed with altitude reflecting local conditions at low altitude plots and meso-scale synoptic conditions having a greater impact at the more exposed 1100 m plot. Both the 300 m and 500 m plots are located in the bottom of the valley and have topographical features that protect them from winds of meso-scale frontal systems. In contrast, the 1100 m plot is positioned on a south facing escarpment, which is exposed to strong south-westerly to southerly winds associated with cold fronts moving through the forest.

Soil. Soil characteristics strongly influence the distribution and biomass of both plants and animals (Sollins 1998, Peres 2000). Identifying which soil factors are most important is very difficult for there is often a strong correlation between soil texture, drainage, nutrients, and surface topography.

Soil properties depend, in part, on the underlying geology and the rates of weathering of this geology. Basalt geology generally weathers to form relatively nutrient rich clay soils (Churchman *et al.* 1995) but over the long timescales that weathering occurs, many minerals are lost, leaving only quartz and simple structured clays. Cations such as calcium, magnesium, potassium, although derived from weathering of the parent rock, are often either leached out of the soil through water percolation or, such

as phosphorus, form insoluble compounds (Baillie 1996). The high temperatures and rainfall often associated with rainforest areas speed up these processes (Chadwick *et al.* 1999, Hedin *et al.* 2003).

Based on this background, soils of Lamington National Park could be described as being deep, old, highly leached and weathered. They are acidic and infertile, with low levels of plant-available phosphorous, calcium, potassium, and magnesium, and high levels of potentially toxic aluminium. Despite these soil nutrient limitations the undisturbed rainforests rely on the recycling of nutrients through the accumulation of a deep organic matter layer and the rapid uptake of nutrients by a dense mat of roots, mycorrhizal fungi and other soil/litter microorganisms (Cuevas 2001). Despite this heavy reliance on organisms to supply nutrients, the soil characteristics still strongly influence (in part) the distribution of plants and animals (Sollins 1998, Peres 2000).

Changes in soil properties with altitude are influenced strongly by microclimate and topography (Proctor *et al.* 2007, Bendix *et al.* 2008, Wilcke *et al.* 2008, Gerold *et al.* 2008). Generally cooler, wetter conditions at higher altitudes reduce biological activity and increase leaching. Steeper profiles encourage runoff and subsurface movement of water downslope. This manifests in the reduction of weatherable nutrients, such as calcium, magnesium, potassium (Table 2) and a decrease in the cation exchange capacity (CEC) at higher altitudes. These generalised trends are seen in this study with a linear decrease in CEC occurring from 31.7 meq/100g at the 300 m plot to 5.85 meq/100g at the 1100 m plot (Table 1). This range in CEC is comparable to those measured in rainforest A horizon soils in Bolivia (<15 cmol kg^{-1}, Schawe *et al.* 2007), Venezuela (Grimm & Fassbender 1981), and the Ecuadorian Andes (Schrumpf *et al.* 2001).

Associated with the loss of alkaline metal ions (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) from the soil is a decrease in soil pH. Rainforest soils typically have a low pH (Veneklaas *et al.* 1990, Tanner *et al.* 1998, Grieve *et al.* 1990, Proctor *et al.* 2007) which frequently decreases with increasing altitude (Schawe *et al.* 2007, Wilcke *et al.* 2008, Proctor *et al.* 2007) as seen in the current study (Table 1). Low soil pH in tropical regions is also thought to reflect the acidic nature of organic matter decomposition and root exudates (Schrumpf *et al.* 2001, Hetsch & Honiesel 1976). Arguably, highly acidic soils may decrease plant species richness and soil fauna biomass (Schawe *et al.* 2007). In the present study, soil at the 1100 m plot was highly acidic and this altitude had the lowest plant diversity of the five studied (Laidlaw *et al.* 2011).

Associated with low pH (below 4.8) is the dominance of free aluminium (Primack & Corlett 2005) and therefore a high exchangeable aluminium content which is commonly found in tropical rainforests (Grieve *et al.* 1990, Schulte & Ruhiyat 1998). The availability of aluminium is intensified through soil acidification at higher altitudes as higher moisture levels leach alkaline metal ions (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) from the soil, further decreasing its pH. This supports the results from IBISCA-Queensland where the highest levels of aluminium were associated with both the lowest levels alkaline metal ions (Table 2) and the highest moisture levels (Table 1). Plants grown in acid soils often suffer aluminium toxicity due to aluminium becoming soluble at low pH thereby impacting on the performance of root systems and manifesting in a variety of nutrient-deficiency symptoms (Mossor-Pietraszewska 1998). In a natural rainforest ecosystem however, the high aluminium content may manifest in a change in floristic composition, with aluminium-tolerant plant species occurring on lowest pH soils.

Accumulation of organic matter at higher altitudes has been noted in other rainforest sites globally and is thought to be associated with frequent water-logging, decreasing temperatures and lower nutrient supply, thereby

reducing organic matter turnover rates due to lower microbial processing (Wilcke *et al.* 2008, Proctor *et al.* 2007). The majority of our results agree with this convention as with increasing altitude we observed increases in organic matter, and soil moisture, a decrease in temperature, reductions in *some* soil nutrients and a decrease in soil acidity. However, we can not be sure that microbial turnover rates are lower at the higher altitudes and therefore responsible for the accumulation of organic matter because this was not specifically tested.

The increase in nitrogen with altitude challenges the argument that high moisture levels and cooler temperatures at the higher altitudes inhibit the microbial turnover of organic matter. This is in contrast to other published studies of rainforest soils along altitudinal gradients (Wilcke *et al.* 2008). Whilst it can be assumed that leaching has been occurring at the study region over the last 20–24 million years, we did not specifically explore the contemporary leaching processes and therefore alternative hypotheses for the high organic matter accumulation at higher altitudes need to be considered.

One such hypothesis is that higher soil organic matter is due to a higher rate of leaf litter fall or a different type of leaf chemistry at the higher altitudes. This is not implausible as the floristic composition of the 1100 m plots markedly differ from those at lower altitudes with an increase in understorey ferns and palms and a canopy dominated by the Gondwanan tree species, *Nothofagus moorei* (see Laidlaw *et al.* 2011). This tree species is a climate relict, which in Lamington National Park is restricted to a few high altitude locations where temperatures are cooler and moisture levels are higher (Veblen *et al.* 1996). Alternatively, the possibility that ferrolysis may contribute to the destruction of clay minerals should be investigated as an alternative process to leaching (Schawe *et al.* 2007), and may partially explain the higher than expected nitrogen values at the highest altitudes.

To address these anomalies, further studies need to investigate the impacts of leaching on contemporary ecosystem processes by measuring soil moisture over a longer time period and at numerous depths through the soil profile. A greater understanding of the role of microbial turnover at the various altitudes will assist in identifying why organic matter accumulates at higher altitudes and this will be aided by measuring C/N ratios, as well as differences in leaf chemistry which may influence the soil microbial community.

CONCLUSIONS

This study aimed to describe the micrometeorological properties and soil characteristics associated with an 800 metre altitudinal gradient at Lamington National Park, thereby providing an abiotic context for other IBISCA-Queensland research projects assessing and predicting the patterns of their focus taxa along the gradient. A year-long microclimate monitoring program investigating parameters both in the canopy and understorey at five altitudes is presented and related to changes in soil conditions collected at one point in time. Microclimate data clearly showed that higher altitudes were cooler, had less temperature variability and were moister. Topography is an important driver of patterns of moisture distribution along with gradient, with the higher altitudes intercepting onshore moisture laden breezes allowing for increased moisture capture at these sites via cloud stripping. Topography and aspect at the lower altitude sites influenced local temperatures, particularly in winter, when cold air drainage and low solar radiation levels reduced minimum temperatures below those at higher altitudes. Soil properties generally reflected the climate data, in particular higher moisture and cooler temperatures experienced at the higher altitudes. This produced a general decrease in nutrients and pH with increased altitude. In contrast, soil moisture, organic matter content and soluble aluminium increased with increasing altitude. These trends

are consistent with other studies and suggest that leaching of nutrients caused by higher moisture levels at the higher altitudes is highly probable and that the build up of organic matter may reflect low microbial turnover rates due to cooler, wetter conditions. However further experimentation is required to test this hypothesis.

This study has demonstrated that climate and soil clearly differ with altitude and that these may be important drivers of identified differences between the vegetation of low and high altitude sites (Laidlaw *et al.* 2011). Other taxa studied in the IBISCA-Queensland project may also be directly influenced by these abiotic parameters or indirectly via the impacts they have on vegetation. Under climate change scenarios, atmospheric drying is likely to have a significant impact on the available moisture in this rainforest, impacting both soil and biological processes. The acquisition of new experimental data on the contribution that cloud and fog events have in delivering moisture to soil and vegetation will significantly enhance our ability to simulate changes in spatio-temporal patterns of biota in response to climate change.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. The work reported here required the assistance of countless volunteers over the two year life span of IBISCA-Queensland, their contributions are greatly appreciated. We thank Drs. Nick Webb and Jo Burton for their invaluable comments on the original manuscript.

LITERATURE CITED

Baillie, I.C. 1996. Soils of the humid tropics. Pp. 256-286. *In*, Richards, P.W., Walsh, R.P.D, Baillie, I.C. & Greig-Smith, P. (eds), *The Tropical Rain Forest: an Ecological Study*. (Cambridge University Press: Cambridge).

Barry, R.G. 1992. *Mountain Weather and Climate* (2nd ed.). (Routhledge: London/New York).

Beckmann, G.G. & Thompson, C.H. 1976. The soils. Pp. 7-10. *In*, Monroe, R. & Stevens, N.C. (eds), *The Border Ranges, a Land Use Conflict in Regional Perspective*. (The Royal Society of Queensland: Brisbane).

Bendix, J., Rollenbeck, R., Richter, M., Fabian, P. & Emck, P. 2008. Climate. Pp. 63-73. *In*, Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador*. (Springer-Verlag: Berlin Heidelberg).

Bureau of Meteorology. 2008. http://www.bom.gov.au/jsp/ncc/cdio/weatherData/

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J. & Hedin, L.O. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* **397**: 491-497.

Chen, I.C., Shiu, H.J., Benedick, S., Holloway, J.D., Cheye, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 1479-1483.

Churchman, G.J., Fitzpatrick, R.W. & Eggleton, R.A. 1995. *Clays: Controlling the Environment*. (CSIRO Publishing: Melbourne).

Cuevas, E. 2001. Soil versus biological controls on nutrient cycling in terra firme forests. Pp. 53-67. *In*, McClain, M.E., Victoria, R.L. & Richey, J.E. (eds), *The Biogeochemistry of the Amazon Basin*. (Oxford University Press: Oxford).

FAO. 1998. *World Reference Base for Soil Resources*. (Food and Agriculture Organization of the United Nations: Rome).

Gerold, G., Schawe, M. & Bach, K. 2008. Hydrometeorologic, pedologic and vegetation patterns along an elevational transect in the montane forest of the Bolivian Yungas. *Erde* **139**: 141-168.

Graham, B.W. 2001. *Tweed Volcanic Region: 360 Million Years Ago to the Present Day*. (B.W. Graham: Tweed Heads).

Grieve, I., Proctor, J. & Cousins, S. 1990. Soil variation with altitude on Volcan Barva, Costa Rica. *Catena Supplement* **17**: 525-534.

Grimm, U. & Fassbender, H.W. 1981. Ciclos bioquimicas en um ecosistema forestal de los Andes Occidentales de Venezuela. I. Inventario de las reservas organicas e minerales (N, P, K, Ca, Mg, Fe, Al, Na). *Turrialba* **31**: 27-37.

Hedin, L.O., Vitousek, P.M. & Matson, P.A. 2003. Nutrient losses over four million years of tropical forest development. *Ecology* **84**: 2231-2255.

Hetsch, W. & Hohiesel, H. 1976. Standorts-und Vegetationsgliederung in einem tropischen Nebelwald. *Allgemeine Forst- und Jagdzeitung* **147**: 200-208.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**: 489-513.

Hutley, L.B., Doley, D., Yates, D.J. & Boonsaner, A. 1997. Water balance of an Australian subtropical rainforest at altitude: the ecolological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany* **45**: 311-329.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55**(2): 271-290.

McDonald, W.J.F. & Whiteman, W.F. 1979. *Moreton Region Vegetation Map Series: Explanatory Booklet for the Murwillumbah Sheet.* (Botany Branch Qld Department of Primary Industries: Brisbane).

Morand, D.T. 1996. *Soil landscapes of the Murwillumbah-Tweed Heads 1:100 000 sheet.* (Department of Land and Water Conservation: Sydney).

Mossor-Pietraszewska, T. 1998. Effect of aluminium on plant growth and metabolism. *Acta Biochimica Polonica* **63**: 673-686.

Northcote, K.H. 1979. *A Factual Key for the Recognition of Australian Soils.* (Rellium Technical Publications: Glenside).

Peres, C.A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* **14**: 240-253.

Primack, R.B. & Collet, R. 2005. *Tropical Rain Forests: an Ecological and Biogeographical Comparison.* (Blackwell Publishing: Cornwell).

Proctor, J., Edwards, I.D., Payton, R.W. & Nagy, L. 2007. Zonation of forest vegetation and soils of mount Cameroon, West Africa. *Plant Ecology* **192**: 251-269.

Rayment, G.E. & Higginson, F.R. 1992. *Australian Laboratory Handbook of Soil and Water Chemical Methods.* (Inkata Press: Melbourne).

Reeder, M.J. & Smith, R.K. 1992. Australian spring and summer cold fronts. *Australian Meteorology Magazine* **41**: 101-124.

Richards, P.W. 1996. *The Tropical Rain Forest.* (Cambridge University Press: Cambridge).

Schawe, M., Glatzel, S. & Gergold, G. 2007. Soil development along an altitudinal transect in a Bolivian tropical montane rainforest: podzolization vs. hydromorphy. *Catena* **69**: 83-90.

Schrumpf, M., Guggenberger, G. & Valarezo, C. 2001. Tropical montane rain forest soils. *Die Erde* **132**: 43-59.

Schulte, A. & Ruhiyat, D. 1998. *Soils of Tropical Forests Ecosystems: Characteristics Ecology and Management.* (Springer-Verlag: Berlin Heidelberg).

Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* **79**: 23-30.

Stevens, N.C. 1976. Geology and landforms. Pp. 1-6. *In*, Monroe, R. & Stevens, N.C. (eds), *The Border Ranges, a Land Use Conflict in Regional Perspective.* (The Royal Society of Queensland: Brisbane).

Sturman, A.P. & Tapper, N.J. 2006. *The Weather and Climate of Australia and New Zealand.* (Oxford University Press: Melbourne).

Tanner, E., Vitousek, P. & Cuevas, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* **79**: 10-22.

Veblen, T.T., Hill, R.S., & Read, J. (eds) 1996. *The Ecology and Biogeography of Nothofagus forests.* (Yale University Press: New Haven, London).

Veneklaas, E. & van Ek, R. 1990. Rainfall interception in two tropical montane rain forests, Columbia. *Hydrological Processes* **4**: 311-326.

Wilcke, W., Yasin, S., Schmitt, A., Valarezo, C. & Zech, W. 2008. Soils along the altitudinal transect and in catchments. Pp. 75-85. *In*, Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador.* (Springer-Verlag, Berlin Heidelberg).

Williams, S.E., Bolitho, E.E. & Fox, S. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**: 1887-1892.

Willmott, W. 2004. *Rocks and Landscapes of the National Parks of Southern Queensland.* (Geological Society of Australia (Queensland Division): Brisbane).

Subtropical rainforest turnover along an altitudinal gradient

Melinda J. LAIDLAW

Queensland Herbarium, Biodiversity and Ecosystem Sciences, Department of Environment and Resource Management, Toowong, Qld 4066, Australia. Email: Melinda.Laidlaw@derm.qld.gov.au

William J.F. McDONALD

Queensland Herbarium, Biodiversity and Ecosystem Sciences, Department of Environment and Resource Management, Toowong, Qld 4066, Australia.

R. John HUNTER

Lowanna, NSW 2450, Australia.

Roger L. KITCHING

Environmental Futures Centre and Griffith School of the Environment, Griffith University, Nathan, Qld 4111, Australia.

Citation: Laidlaw, M.J., McDonald, W.J.F., Hunter, J.R. & Kitching, R.L. 2011 12 20: Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum – Nature* 55(2): 271-290. Brisbane. ISSN 0079-8835.

ABSTRACT

The rainforests of south-east Queensland and northern New South Wales are highly diverse and floristically and structurally complex. This diversity is due, in part, to regional variation in soil and parent geology, climate and topography. Patterns in regional species composition were investigated along an altitudinal transect from 300 to 1100 m elevation in Lamington National Park, south-east Queensland. This study also relates subtropical rainforest composition to soil variables and to the environmental correlates of altitude, namely temperature and moisture. Twenty-nine climatic and nine soil variables were correlated with floristic variation between altitudes. Twelve species groups were also identified from the 282 vascular plant species recorded along the transect. These baseline data will form the benchmark against which future changes in the forest can be monitored. The use of adjacent altitudes as surrogates for adjacent climates can also provide a useful insight into the potential impacts of a changing climate. ❐ *altitudinal gradient, climate change, compositional turnover, subtropical rainforest, surrogacy.*

The subtropical rainforests of south-east Queensland and northern New South Wales are a living link to our botanical past. They support subtropical through to cool temperate biota and have done so throughout the climatic fluctuations of the Late Tertiary and Quaternary (Adam 1987). This continuity of climate has allowed the persistence of primitive plant families (Winteraceae, Eupomatiaceae, Annonaceae, Trimeniaceae, Monimiaceae, Atherospermataceae and Lauraceae) which have undergone little evolutionary change since Gondwanan times (McDonald 2010; Floyd 1990a). These rainforests also host 42 genera of primitive angiosperms and

gymnosperms (Floyd 2008), relictual and endemic species, as well as rare and threatened flora (McDonald 2010).

Subtropical rainforest is particularly well represented in Australia and extends from approximately 21°–35° latitude (based on the prominence of notophyll and microphyll canopy leaves) (Webb 1959). These forests have been described and classified under various schemes at both continental (Webb 1978, 1968, 1959) and state levels (Sattler & Williams 1999; Baur 1964). Lamington National Park supports several structural types of rainforest, three of which were examined in this study and described below. The approximate equivalents between classification schemes are also included below.

Araucarian Complex Notophyll Vine Forest (ANVF) (Webb 1978, 1968, 1959)/Qld Regional Ecosystem (RE) 12.8.4 (Sattler & Williams 1999)/Dry rainforest (Floyd 1990b; Baur 1964). This structural form occurs on basalt soils on the northern and western slopes of the Lamington Plateau and on shallow rocky soils on steep slopes. ANVF is a subtype of the more extensive complex notophyll vine forest (CNVF) dominant in the region. It differs from other forms of CNVF in supporting emergent hoop pine, *Araucaria cunninghamii*. This structural type is tolerant not only of a lower annual rainfall, but a marked dry season between spring and early summer (McDonald & Whiteman 1979).

Complex Notophyll Vine Forest (CNVF) (Webb 1978, 1968, 1959)/RE 12.8.3 and 12.8.5 (Sattler & Williams 1999)/Subtropical rainforest (Floyd 1990b; Baur 1964). CNVF occurs on basalt soils and Lamington National Park supports some of the most extensive and best developed stands of this rainforest type in the region. It is both floristically and structurally complex. There are two broad subtypes, the distributions of which are associated with altitude. Warm subtropical CNVF/RE 12.8.3, generally occurs below 600–700 m a.s.l., particularly in valleys. This forest type can grade into ANVF on steep slopes and on drier aspects (McDonald & Whiteman 1979). Cool subtropical CNVF/RE 12.8.5 generally occurs at altitudes above 600–700 m, although a broad ecotone of high floristic diversity between these two subtypes can occur (Laidlaw *et al.* 2000). All forms of CNVF support robust and woody lianes, a diverse community of vascular epiphytes, canopy species with plank buttresses and compound, entire leaves, as well as other life forms such as palms and climbing aroids (*Pothos longipes*) (Webb 1959).

Microphyll Fern Forest (MFF) (Webb 1978)/RE 12.8.6 (Sattler & Williams 1999)/Cool temperate rainforest (Floyd 1990b; Baur 1964). MFF occurs on the high plateaus and mountain tops at altitudes over 1000 m. Rainfall at this altitude is supplemented by the interception of water from clouds that occur frequently with onshore winds (Floyd 2008). This forest is typically dominated by *Nothofagus moorei* (Nothofagaceae), a species whose extent has contracted and moved south and upslope, along with cold and wet microclimates (Hopkins *et al.* 1976; Webb 1964). These forests are without plank buttress forming species or woody lianes. Instead, they support prolific mossy epiphytes, tree and ground ferns and tree species with simple, toothed leaves (McDonald & Whiteman 1979).

The distribution of these three structural types of rainforest at Lamington National Park are known to be correlated with the environmental features of topography (particularly aspect), climate, soil nutrient status, soil depth and moisture content (Adam 1987; Hopkins *et al.* 1976; Webb 1969, 1968). The response of species groups to these environmental variables is complex and interactions between them are likely (Adam 1987). It can be very difficult to attribute rainforest distribution to any one factor, however, general trends can be identified. Broadly speaking, CNVF (and subtypes) occur in a mesothermal environment with annual mean maximum temperatures of 18–22°C and an annual mean minimum of 5°C. By

comparison, MFF is found in a microthermal environment with an optimum annual mean maximum temperature of 10-12°C and an annual mean minimum of 0°C (Floyd 1990a; Adam 1987). Such microthermal conditions in the study region are restricted to altitudes over 1000 m and to elevated gullies, where cold air drainage allows the downslope extension of these conditions. The downslope extension of MFF, under appropriate moisture regimes, is likely restricted by either intolerance of higher temperatures (Fraser & Vickery 1939), or by the superior competitive ability of CNVF species (Dolman 1982). The upslope extension of CNVF is restricted by its susceptibility to frost events tolerated by species such as *Nothofagus moorei* (Adam 1987; Dolman 1982).

The moisture regime is a result of the complex interaction between precipitation, aspect, slope, soil parent material and soil depth (Adam 1987). ANVF occurs where annual rainfall ranges between 660–1100 mm, CNVF is found where it exceeds 1300 mm, while MFF is found where annual rainfall is over 1750 mm, with the input of up to an additional 50% of this annual rainfall from fog drip (Floyd 2008, 1990; Hutley *et al.* 1997; King 1980; Fisher & Timms 1978). Rainfall seasonality is also important. ANVF is able to withstand a pronounced dry season. CNVF requires a largely uniformly distributed rainfall with a summer peak when evaporative potential is highest and MFF requires consistently moist conditions from both rainfall and regular contact with cloud and fog (Floyd 2008, 1990). The availability of these moisture inputs to rainforest species also depends quite strongly on the geological history of the region.

The volcanic strata underlying Lamington National Park were laid down in three major series of eruptions emanating from Mt Warning to the south. The Beechmont Basalt is overlain by the Binna Burra Rhyolite and scattered pyroclastic vents, which was then capped by the later Hobwee Basalt (Stevens 1976). The current erosion caldera is a result of the differential weathering of these strata for 20 million years (Willmott 1992). Basalts generally weather to red krasnozem soils which are fine textured with a high water holding capacity, acidic and low in soil nutrients, except for those stored in the surface horizons (Beckmann & Thompson 1976). Subtle differences in basalt chemical composition, differential weathering characters and age of weathering surfaces, in conjunction with varied topography and the resulting microclimate has resulted in a wide variety of soil types even on this one geology (Beckmann & Thompson 1976). The multiple basalt flows and their subsequent weathering has also resulted in step and bench sequences down the slopes (Turner 1976) and associated variations in soil depth.

According to Webb (1959), edaphic factors can be just as important in determining community composition and distribution as climatic variables. However, this is a complex interaction and equally for some structural types, edaphic factors are dominated by climate. A forest type which is highly competitive on poor soils under favourable climatic conditions, may be able to tolerate sub-optimal rainfall only on richer soils (Adam 1987). Similarly, CNVF may be able to tolerate poorer soils if rainfall is sufficient and there is no dry season (Adam 1987). High rainfall may also be able to compensate for poorer soils in some cases such as in sheltered, fire protected sites (edaphic compensation) (Floyd 1990a; Webb 1969, 1959).

Subtropical rainforest distribution is greatly impacted by topography (Adam 1987). Aspect is more important at this latitude than in tropical rainforests where the sunlight received annually is similar between northerly and southerly aspects. On the shortest day in winter at Lamington National Park, the sun shines for 10.25 hours (flat plane) and reaches a maximum altitude of 38.42° (Cornwall *et al.* 2009). This low altitude means that much of the forest on southerly slopes and enclosed gullies receives far less than 10 hours of sunlight per day. The forests

tucked below the inner rim of the caldera may receive no direct sunlight at all for extended periods through winter. The southern and eastern aspects are also protected from drying northerly and westerly winds in late winter and spring and from direct solar radiation in the heat of summer, where the midday sun sits almost directly over the forest at an altitude of 85° (Cornwall *et al.* 2009; Floyd 2008). Erosion gullies shelter rainforest from fire, frost and damaging winds, as well as being sites of higher soil nutrients and moisture (Floyd 2008, 1990). Soils also vary significantly between ridges and valleys, generally becoming deeper and higher in soil nutrients and moisture downslope (McKenzie *et al.* 2004). However, on steep slopes, erosion and leaching of soil nutrients may be pronounced (Floyd 2008).

This study seeks to identify current patterns in species composition in the subtropical rainforest communities of south-east Queensland and to relate these patterns to current climatic conditions through the establishment of an altitudinal transect. This baseline will allow changes in floristic composition and their environmental correlates to be tracked over time and will serve as the essential benchmark against which resurveys of the forest will be compared. In addition, we use the current climatic envelopes of adjacent altitudes as a surrogate for climatic variation over time and identify species and groups for which predicted future climatic changes may prove challenging. This transect samples the response of vegetation along two major environmental axes along which human influenced climate is predicted to shift, temperature and moisture.

MATERIALS AND METHODS

Twenty permanently marked 20 m x 20 m vegetation survey plots were established in August 2006 in the Canungra Creek catchment of Lamington National Park, south-east Queensland, Australia. These plots sample several structural types of subtropical rainforest vegetation at five altitudes: 300, 500, 700, 900 and 1100 m a.s.l. Four plots were established at each of these altitudes, with a minimum distance of 400 m along the contour between replicates, and the data for each altitude were pooled. This was done in place of establishing large plots at each altitude, which previous studies (Laidlaw *et al.* 2000) have shown must be at least 80 x 80 m in size before an asymptote is achieved in the species accumulation curve. The plots were located ≥ 50 m from permanent water and away from recent disturbance, however, this was more difficult at 300 and 500 m a.s.l. due to the steep terrain lower in the catchment. All plots were positioned on basic Cainozoic volcanic rocks (Beechmont and Hobwee basalts). Soil samples were collected from each plot, air-dried and analysed for pH, conductivity and nutrient status. Soil analysis techniques are described in Strong *et al.* (2011).

The transect traverses a steep moisture and temperature gradient, where lower altitudes generally experience hotter and drier conditions, while upland sites generally experience colder and moister conditions. These trends can be strongly influenced by aspect. The establishment of all survey plots within a single catchment and, as far as possible, maintaining a common north-north-westerly aspect, attempted to reduce this variation. All established trees ≥ 5 cm diameter at breast height (dbh: measured at 1.3 m height or directly above buttresses or below bole deformities) were numbered and measured for diameter and height and were identified to species by the Queensland Herbarium (see Bostock & Holland (2007) for species authorities). Multi-stemmed species were treated as separate individuals wherever stems were ≥ 5 cm dbh. Where vines and epiphytes obstructed the bole, these were gently lifted to allow accurate dbh measurement. All other vascular species on each plot were identified and given a cover score.

Multivariate analyses were conducted on data pooled across four 20 m x 20 m plots per altitude.

The pattern analysis software WinPATN (Belbin *et al.* 2003) was used to examine the association between altitude and floristic composition along the transect. The Bray-Curtis dissimilarity metric (Bray & Curtis 1957) was applied to presence/absence data and used to determine the floristic dissimilarity between altitudes. A two-step procedure, based on the Bray-Curtis dissimilarity metric (Belbin *et al.* 2003), was used to examine the relationships between species based on the altitudes at which they were recorded. The groups resulting from both associations are displayed in a two-way table. The data were classified using unweighted pair group arithmetic averaging (UPGMA) (β value = -0.1). Semi-strong hybrid multidimensional scaling ordination (SSH MDS) was used to depict the association between altitudes based on their floristic composition in two-dimensional space (Belbin *et al.* 2003) using a dissimilarity cutoff value of 0.9. Minimum spanning trees are used to display the floristic links between pairs of altitudes surveyed along the transect.

Principal axis correlation (PCC) (Belbin *et al.* 2003) was used to calculate the correlation between sampled altitudes in ordination space and selected intrinsic (species) and extrinsic (climatic, edaphic and topographic) variables for the transect. Thirty-five climatic variables were modelled using the Bioclim climate modelling package (Houlder *et al.* 2000), applied to an 80 m digital elevation model. A Monte-Carlo permutation test (Belbin *et al.* 2003), MCAO (1000 permutations) was used to test the significance of the relationship between altitudinal groups, their constituent species and extrinsic variables. Biplots of these significant extrinsic variables were overlaid on the ordination.

RESULTS

Recorded from the 20 plots along the transect were a total of 282 species, including 1218 tree stems (≥5 cm dbh) of 115 species, 90 genera and 37 families (including one species of tree fern and one species of tree palm). The study also recorded 10 species of shrub, 59 species of vine, 18 species of herb, 13 species of ground fern, 13 species of orchid, 17 species of 'epiphyte' (15 ferns, one climber and one true epiphyte). The remaining 37 species recorded were understorey tree species (<5 cm cutoff) and seedlings of tree species not recorded in the canopy.

The association between the sites at five different altitudes along the transect based on the plant communities recorded was examined using Bray-Curtis dissimilarity (Fig. 1). The high altitude sites (900 and 1100 m) were found to be dissimilar from the mid-low altitude sites (700-300 m) (BC = 0.77). The 900 m and 1100 m sites had a Bray-Curtis dissimilarity of 0.53. The two most closely related altitudes were 500 m and 700 m (BC = 0.27) and these were then joined with the 300 m altitude sites with a BC dissimilarity of 0.43. These results of the classification suggest that the altitudinal transect, and the large amount of environmental variation captured, contained four distinct rainforest communities, with the 500 m and 700 m sites representing the same community.

The 282 species were classified according to their occurrence at different altitudes using a two-step procedure (Belbin 2003). Twelve species groups were identified from the resulting dendrogram and are presented along with the four altitudinal groups in a two-way table (Table 1). A MCAO significance test on a principal components correlation for the transect showed that 72 species (25 tree species, 17 species of climber, three species of herb, five species of ground fern, one tree fern, five species of epiphytic orchid, five species of epiphytic fern and 11 species of tree seedling) were significantly (MCAO ≤ 1%) correlated with altitude. These species are highlighted as significant in Table 1.

A MCAO significance test of a principal components correlation for the transect showed that 29 climate variables were significantly (MCAO ≤1%) correlated with floristic composition. Of

these climate variables, 11 were temperature-based, three precipitation, seven radiation and eight moisture-based. Figure 2 shows 10 of the 29 climate variables indicative of the trends. Higher temperatures, radiation and pronounced moisture seasonality were associated with the lower altitude sites, whilst higher precipitation (particularly during the winter dry season) was strongly associated with the high altitude sites. Radiation seasonality was highest at the 1100 m sites.

A MCAO significance test of a principal components correlation for the transect showed that nine soil variables were significantly (MCAO ≤1%) correlated with the altitudinal groupings. PH decreased with increasing altitude (Strong *et al.* 2011) and was found to be significantly correlated with the altitudinal groupings of plant communities (Fig. 3). Soil magnesium, potassium, sodium, chloride and sulphur content were found to be significantly correlated with plant community composition (Fig. 3). Sulphur and chloride content increased with altitude, while all other soil variables decreased with altitude (Strong *et al.* 2011). Sodium base saturation percentage (BSP) was found to be significantly correlated with vegetation communities at different altitudes (Fig. 2) and was highest at high altitude.

DISCUSSION

This study recorded approximately half of the 320 rainforest tree species recorded in the region (Floyd 1990a; W.J.F. McDonald personal observation). Four identifiable rainforest structural types were surveyed along the transect and these correspond to the structural types previously identified by Webb (1978, 1968, 1959), Sattler & Williams (1999) and Baur (1964). Twelve species groups were also identified from the 20 plots, each responding to the environmental conditions at the altitudes at which they occur.

Species group (a) is composed of ANVF specialists, recorded only from the 300 m sites. This forest type has been extensively cleared within the region for agriculture and species such as *Toona ciliata* and *Araucaria cunninghamii* targeted for logging. These low altitude species are able to withstand extended dry periods and associated high evapotranspiration rates. This group of species could be expected to expand its distribution upslope should predicted climate warming and regional drying occur (Cai *et al.* 2005).

Species group (b) comprises those species occurring in both the warm and cool subtypes of CNVF, where evapotranspiration is lower due to increased moisture inputs and lower temperatures than in ANVF. Species group (c) is a mixed group which consists of a number of smaller species groups lumped together here due to the arbitrary splitting of the dendrogram at 12 groups. Some species in this group are distributed along all or much of the length of the altitudinal transect and are largely generalists in that they are able to persist under a variety of conditions. Some occurred in all structural forest types on the transect, others in all types except ANVF or MFF. Some species in group (c) were found to have disjunct distributions. This is a sampling artefact, however, as these species have previously been recorded at intermediate altitudes. Five species in this group (*Eupomatia laurina, Helicia glabriflora, Melodinus australis, Solanum inaequilaterum* and *Geitonoplesium cymosum*) were found only in the cooler types above 700 m and would form their own group at a finer scale of analysis. The two-way table lets us, however, identify that the five species in this finer group are perhaps more sensitive to drier conditions at lower altitudes and may be good indicators of increasing moisture stress in these forests.

Species group (d) are species found in all types of notophyll vine forest, but are absent from MFF. All of the species in this group, many of them tree species, were found to be

significant in the MCAO. These species may not be able to tolerate the low levels of solar radiation, periodic soil waterlogging, higher acidity or colder soil temperatures at the highest altitude. This group includes three of the dominant species in these subtropical rainforests, *Argyrodendron actinophyllum*, *A. trifoliolatum* and *Pseudoweinmannia lachnocarpa*.

Species in group (e) are restricted to the warm CNVF forest at 500 m and 700 m. Forests at these two altitudes were found to be more similar than any other. The nominal altitude for distinguishing between warm and cool CNVF is 600 m, however, in this catchment, warm CNVF appears to extend higher with a broad ecotone into cool CNVF. This may be due to the generally northern aspect of the study transect.

Species group (f) includes ten species recorded only at 700 m. These ten species were found to be significantly correlated with altitude. The sites established at 700 m were located midslope with a mean slope of 11.25° (± SE 1.1). Steep slopes often have shallower, less mature soils with a reduced ability to hold moisture and soil nutrients (Turner 1976). These ten species could experience increasing stress under predicted climate change scenarios. Alternatively, their tolerance for difficult conditions may pre-adapt them for expansion.

Species group (g) consists of species recorded only from 300 m and 500 m, many of which are trees or tree seedlings. Sites at both of these altitudes were necessarily located approximately 50 m from a creek line. Soils along the creek at 300 m and 500 m were grey-brown and possibly impacted by alluvial processes during flood events (Strong *et al.* 2011). These species may be utilising the higher clay content and nutrients in the alluvial soils at these sites.

Species group (h) are species recorded solely at the 500 m sites. Only 3 species in this group are tree species and almost half are climbers. This, along with the location of these sites low in the valley close to a creek line and on steep slopes, may indicate a higher return rate of disturbance than at other altitudes.

Species recorded only from 900 m and 1100 m form species group (i). These species may have higher moisture requirements than those at lower altitudes and be tolerant of low solar radiation and lower temperatures. Species in group (j) were recorded only at 900 m. Species such as *Acradenia euodiiformis*, may be an indicator of a severe storm which passed through this area in 1983 (Olsen & Lamb 1984), although this study intentionally avoided the worst of this disturbance. This altitude also sits at the level of the current cloud base on moderately humid days and may be sensitive to moisture stress in the event that the cloud base rises along with increasing atmospheric temperatures. Species in this group may serve as sentinel species to identify future impacts of a drying climate (Laidlaw *et al.* 2011). For example, *Tasmannia insipida* has been shown to be a good indicator of the presence of cloud in the Mackay area (W.J.F. McDonald personal observation).

Species group (k) are those species found only at mid to low altitudes (≤ 700m a.s.l.). Species such as *Lophostemon confertus* (Myrtaceae) were recorded in the canopy and tell the tale of when these forests were more open than they are currently as this species cannot persist under a closed canopy. These forests may be younger than those upslope and resemble a forest type extensive during drier times as recent as 500 years ago (Turner 1976). This and the other species groups of mid to low altitudes (h, g, f, e and a) are likely to be more tolerant of higher temperatures, lower moisture inputs and higher evapotranspiration than those at 900 m and above.

Species group (l) are all MFF specialists, all significantly correlated with altitude and occur nowhere else along the transect. These species are tolerant of the low solar radiation, high soil acidity, soil water logging, low temperatures and occasional frosts and snow found at altitudes

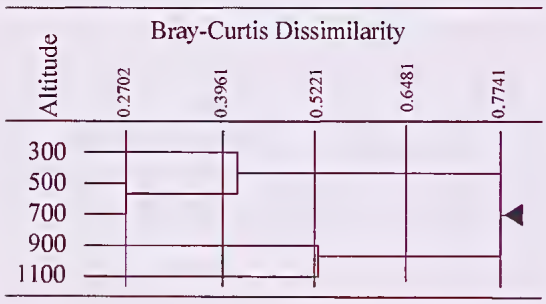


FIG. 1. Bray-Curtis dissimilarity dendrogram of altitudinal groups (300, 500, 700, 900 and 1100 m a.s.l.) based on floristic composition.

above 1000 m. Species such as *Nothofagus moorei*, *Quintinia sieberi* and *Callicoma serratifolia* are components of relictual Gondwanan rainforest (Webb *et al.* 1986). These forests support many high altitude endemic species which are at the highest risk of extinction from a warming climate. As such, these species will be important indicators of change in this forest type and may require intervention for their continued survival.

Soil variables, in conjunction with their climatic and topographic drivers, were found to be significantly correlated with floristic differences between altitudes. All twelve species groups were found on acidic soils (pH < 6.5). Acidity increased with altitude (Strong *et al.* 2011) in response to increased rainfall and subsequent leaching (McKenzie *et al.* 2004). Soil pH is known to impact on soil structure, weathering and humification (Larcher 1980). It is also known to impair the uptake of some soil nutrients such as calcium, magnesium and potassium (McKenzie *et al.* 2004), all three of which were found to be significantly correlated with altitudinal groupings and were found at higher concentrations at lower altitudes. Aluminium is preferentially liberated in acidic soils (Larcher 1980) and was found to increase with altitude (Strong *et al.* 2011). Aluminium can reduce the availability of calcium to

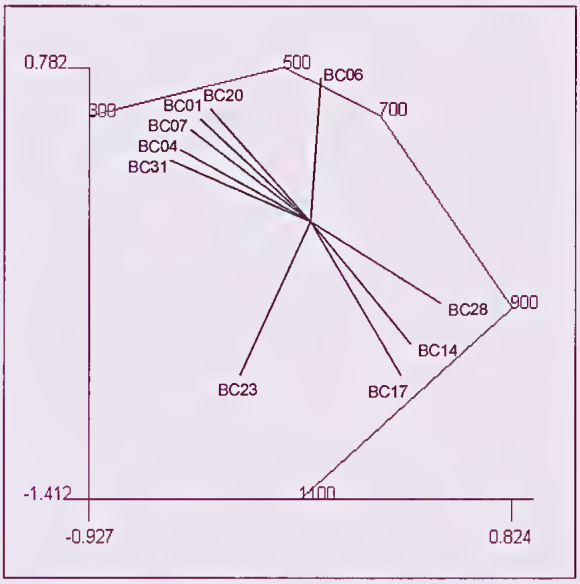


FIG. 2. Semi-strong hybrid multidimensional scaling ordination (stress = 0.08) of altitudes based on floristic composition with minimal spanning tree, and biplot of selected correlated climatic variables identified by the MCAO significance test. BC01, annual mean temperature; BC04, temperature seasonality; BC06, minimum temperature of the coldest period; BC07, temperature annual range; BC14, precipitation of the coldest period; BC17, precipitation of the driest quarter; BC20, annual mean radiation; BC23, radiation seasonality; BC28, annual mean moisture index; BC31, moisture index seasonality.

plants (Graham 2001) and species which prefer calcareous soils, such as those of CNVF (Floyd 2008), are also often sensitive to aluminium (Larcher 1980). It is possible that the CNVF communities found at mid to low altitudes in this study are in part excluded from higher altitudes by this lowering of calcium availability.

Base saturation percentage (BSP) is the portion of soil cation exchange capacity (CEC) accounted for by exchangeable bases and is an indicator of soil fertility (Rayment & Higginson 1992). Bases such as sodium can be depleted from soil through leaching, particularly under the warm and moist conditions often found

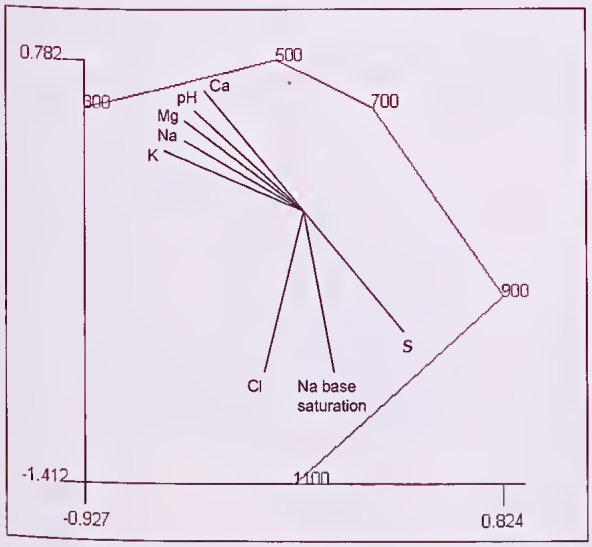


FIG. 3. Semi-strong hybrid multidimensional scaling ordination (stress = 0.08) of altitudes based on species composition with minimal spanning tree, and biplot of selected correlated soil variables identified by the MCAO significance test. (Ca, Calcium; Mg, Magnesium; Na, Sodium; K, Potassium; Cl, Chloride; S, Sulphur).

in rainforests (Rayment & Higginson 1992). This process is accentuated at higher, wetter altitudes. The higher altitude forests were also significantly associated with higher chloride and sulphur levels.

The identification of climatic variables significant in determining current species groups and distributions can be complicated by the long generation times of rainforest species, particularly trees. The conditions under which an individual germinated and established may be quite different from current climatic conditions. This may become increasingly difficult as the climate these forests will face in the near future will be both hotter and drier than those the forest is currently experiencing (Cai *et al.* 2005). For some species and communities, edaphic variables may be able to compensate to a degree, as will dispersal into cooler and moister altitudes and aspects. This study, along with continued monitoring along the altitudinal transect, will assist with change detection and management of these important forests.

ACKNOWLEDGEMENTS

In respectful memory of Len Webb (1920-2008).

A project such as IBISCA-Queensland cannot function without major funding. We are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Global Canopy Programme, NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. We also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We are grateful to all these sources without which the project would not have been possible. O'Reilly's Rainforest Resort and the Mt Cainbable Cabins provided accommodation and sustenance. For technical, administrative and field assistance, our sincerest thanks go to Sarah Boulter, David Putland, Hugh and Nan Nicholson, Alice Yeates, Sarah Maunsell, Don Butler, Sandy Pollock, Arnon Accad, Rosemary Niehus, Kyran Staunton, Gillian Naylor, Jana Crooks and Heather Christensen.

TABLE 1. Two-way table of twelve vascular plant species assemblages recorded for each of four altitudinal groups (300, 500 & 700, 900, 1100 m a.s.l.). * indicates species significant in driving altitudinal groups (MCAO ≤ 1%). # indicates non-native or naturalised species. Abbreviations for life forms are as follows: *t*, tree; *ts*, tree seedling/understorey tree; *tf*, tree fern; *p*, palm; *sh*, shrub; *h*, herb; *f*, fern; *c*, climber; *e*, epiphyte; *o*, orchid; *ec*, epiphytic climber; *ef*, epiphytic fern; *eo*, epiphytic orchid.

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
a		*Abutilon oxycarpum*	Malvaceae	*sh*	*				
36 species		*Toona ciliata*	Meliaceae	*ts*	*				
		Syzygium francisii	Myrtaceae	*t*	*				
		Alchornea ilicifolia	Euphorbiaceae	*t*	*				
		Adiantum hispidulum	Adiantaceae	*f*	*				
		Asplenium attenuatum	Aspleniaceae	*ef*	*				
		Aneilema acuminatum	Commelinaceae	*h*	*				
		Castanospermum australe	Fabaceae	*t*	*				
		Carissa ovata	Apocynaceae	*sh*	*				
		Carex sp.	Cyperaceae	*h*	*				
		Capparis sarmentosa	Capparaceae	*c*	*				
		Calamus muelleri	Arecaceae	*c*	*				
		Deeringia amaranthoides	Amaranthaceae	*h*	*				
		Daphnandra apatela	Atherospermaceae	*t*	*				
		Dendrocnide excelsa	Urticaceae	*t*	*				
		Elaeocarpus obovatus	Elaeocarpaceae	*ts*	*				
		Ficus obliqua	Moraceae	*t*	*				
		Ficus macrophylla forma macrophylla	Moraceae	*t*	*				
		Ficus fraseri	Moraceae	*t*	*				
		Excoecaria dallachyana	Euphorbiaceae	*t*	*				
		Jasminum simplicifolium subsp. *australiense*	Oleaceae	*c*	*				
		Ixora beckleri	Rubiaceae	*t*	*				
		Hippocratea barbata	Celastraceae	*c*	*				
		Guilfoylia monostylis	Surianaceae	*t*	*				
		Mallotus discolor	Euphorbiaceae	*ts*	*				
		Mallotus claoxyloides	Euphorbiaceae	*t*	*				
		Morinda cunthoides	Rubiaceae	*c*	*				
		Mischocarpus anodontus	Sapindaceae	*t*	*				
		Marsdenia pleiadenia	Apocynaceae	*c*	*				
		Oplismenus aemulus	Poaceae	*h*	*				

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
a cont...		*Olea paniculata*	Oleaceae	*ts*	*				
		Pavetta australiensis	Rubiaceae	*ts*	*				
		Psydrax lamprophylla forma *lamprophylla*	Rubiaceae	*ts*	*				
		Podocarpus elatus	Podocarpaceae	*ts*	*				
		Sterculia quadrifida	Sterculiaceae	*ts*	*				
		Siphonodon australis	Celastraceae	*t*	*				
b 23 species	*	*Acmena ingens*	Myrtaceae	*ts*		*	*	*	
	*	*Dendrobium gracilicaule*	Orchidaceae	*eo*		*	*	*	
	*	*Dictymia brownii*	Polypodiaceae	*ef*		*	*	*	
	*	*Elattostachys xylocarpa*	Sapindaceae	*t*		*	*	*	
	*	*Guioa semiglauca*	Sapindaceae	*ts*		*	*	*	
	*	*Neolitsea australiensis*	Lauraceae	*t*		*	*	*	
	*	*Neolitsea dealbata*	Lauraceae	*ts*		*	*	*	
	*	*Morinda jasminoides*	Rubiaceae	*c*		*	*	*	
	*	*Mischocarpus australis*	Sapindaceae	*ts*		*	*	*	
	*	*Piper hederaceum* var. *hederaceum*	Piperaceae	*c*		*	*	*	
	*	*Phaleria clemensiana*	Thymelaeaceae	*t*		*	*	*	
	*	*Ripogonum elseyanum*	Ripogonaceae	*c*		*	*	*	
	*	*Dockrillia teretifolia*	Orchidaceae	*eo*		*		*	
	*	*Harpullia alata*	Sapindaceae	*ts*		*		*	
	*	*Litsea reticulata*	Lauraceae	*t*		*		*	
		Acronychia baeuerlenii	Rutaceae	*ts*			*	*	
		Zanthoxylum brachyacanthum	Rutaceae	*t*			*	*	
		Cinnamomum virens	Lauraceae	*t*			*	*	
		Clerodendrum floribundum	Vitaceae	*ts*			*	*	
		Decaspermum humile	Myrtaceae	*t*			*	*	
		Endiandra muelleri subsp. *muelleri*	Lauraceae	*ts*			*	*	
		Emmenosperma alphitonioides	Rhamnaceae	*t*			*	*	
		Platycerium bifurcatum	Polypodiaceae	*ef*			*	*	
c 38 species		*Alangium villosum* subsp. *polyosmoides*	Cornaceae	*t*	*			*	*
		Asplenium polyodon	Aspleniaceae	*ef*	*		*	*	*
		Melicope micrococca	Rutaceae	*t*	*		*	*	*

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
c cont...		*Smilax australis*	Smilacaceae	*c*	*		*	*	*
		Archontophoenix cunninghamiana	Arecaceae	*p*	*	*	*		*
		Dianella caerulea var. *vannata*	Hemerocallidaceae	*h*	*	*	*		*
		Lastreopsis decomposita	Dryopteridaceae	*f*	*	*	*		*
		Pellaea falcata	Adiantaceae	*f*	*	*	*		*
		Pyrrosia confluens var. *confluens*	Polypodiaceae	*ef*	*	*	*		*
		Asplenium australasicum	Aspleniaceae	*ef*	*	*	*	*	*
		Derris involuta	Fabaceae	*c*	*	*	*	*	*
		Diploglottis australis	Sapindaceae	*t*	*	*	*	*	*
		Dysoxylum fraserianum	Meliaceae	*t*	*	*	*	*	*
		Lomandra spicata	Laxmanniaceae	*h*	*	*	*	*	*
		Pyrrosia rupestris	Polypodiaceae	*ef*	*	*	*	*	*
		Archidendron grandiflorum	Mimosaceae	*t*	*	*		*	
		Pentaceras australe	Rutaceae	*t*	*	*		*	
		Dianella caerulea var. *assera*	Hemerocallidaceae	*h*	*		*	*	
		Rhinerrhiza divitiflora	Orchidaceae	*eo*	*		*	*	
		Citronella moorei	Leptaulaceae	*t*	*			*	
		Austrosteenisia glabristyla	Fabaceae	*c*		*	*	*	*
		Wilkiea huegeliana	Monimiaceae	*t*		*	*	*	*
		Cephalaralia cephalobotrys	Araliaceae	*c*		*	*	*	*
		Cordyline rubra	Laxmanniaceae	*sh*		*	*	*	*
		Denhamia celastroides	Celastraceae	*t*		*	*	*	*
		Linospadix monostachya	Arecaceae	*p*		*	*	*	*
		Psychotria simmondsiana	Rubiaceae	*t*		*	*	*	*
		Pothos longipes	Araceae	*ec*		*	*	*	*
		Sarcopteryx stipata	Sapindaceae	*t*		*	*	*	*
		Cryptocarya erythroxylon	Lauraceae	*t*		*		*	*
		Wilkiea austroqueenslandica	Monimiaceae	*t*		*		*	*
		Microsorum scandens	Polypodiaceae	*ef*		*		*	*
		Eupomatia laurina	Eupomatiaceae	*t*			*	*	*
		Helicia glabriflora	Proteaceae	*t*			*	*	*
		Melodinus australis	Apocynaceae	*c*			*	*	*
		Solanum inaequilaterum	Solanaceae	*sh*			*	*	*
		Geitonoplesium cymosum	Hemerocallidaceae	*c*			*		*

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
c cont...		*Pandorea floribunda*	Bignoniaceae	*c*		*	*		*
d	*	*Authocarapa nitidula*	Meliaceae	*t*	*	*	*	*	
19 species	*	*Trophis scandens* subsp. *scandens*	Moraceae	*c*	*	*	*	*	
	*	*Arthropteris tenella*	Nephrolepidaceae	*ef*	*	*	*	*	
	*	*Argyrodendron trifoliolatum*	Sterculiaceae	*t*	*	*	*	*	
	*	*Argyrodendron actinophyllum* subsp. *actinophyllum*	Sterculiaceae	*t*	*	*	*	*	
	*	*Araucaria cunninghamii* var. *cunninghamii*	Araucariaceae	*t*	*	*	*	*	
	*	*Brachychiton acerifolius*	Sterculiaceae	*t*	*	*	*	*	
	*	*Baloghia inophylla*	Euphorbiaceae	*t*	*	*	*	*	
	*	*Atractocarpus chartaceus*	Rubiaceae	*t*	*	*	*	*	
	*	*Caesalpinia subtropica*	Caesalpiniaceae	*c*	*	*	*	*	
	*	*Cryptocarya obovata*	Lauraceae	*t*	*	*	*	*	
	*	*Diospyros pentamera*	Ebenaceae	*t*	*	*	*	*	
	*	*Embelia australiana*	Myrsinaceae	*c*	*	*	*	*	
	*	*Elaeodendron australe* var. *australe*	Celastraceae	*t*	*	*	*	*	
	*	*Doodia aspera*	Blechnaceae	*f*	*	*	*	*	
	*	*Ficus watkinsiana*	Moraceae	*t*	*	*	*	*	
	*	*Notelaea johnsonii*	Oleaceae	*t*	*	*	*	*	
	*	*Pseudoweinmannia lachnocarpa*	Cunoniaceae	*t*	*	*	*	*	
	*	*Sarcomelicope simplicifolia* subsp. *simplicifolia*	Rutaceae	*t*	*	*	*	*	
e		*Akania bidwillii*	Akaniaceae	*t*		*	*		
14 species		*Tylophora paniculata*	Apocynaceae	*c*		*	*		
		Alocasia brisbanensis	Araceae	*h*		*	*		
		Calanthe triplicata	Orchidaceae	*o*		*	*		
		Daphnandra tenuipes	Atherospermaceae	*t*		*	*		
		Dysoxylum rufum	Meliaceae	*t*		*	*		
		Lastreopsis microsora subsp. *microsora*	Dryopteridaceae	*f*		*	*		
		Parsonsia straminea	Apocynaceae	*c*		*	*		
		Parsonsia longipetiolata	Apocynaceae	*c*		*	*		
		Pseuderanthemum variabile	Acanthaceae	*h*		*	*		
		Pollia crispata	Commelinaceae	*h*		*	*		
		Scolopia braunii	Flacourtiaceae	*t*		*	*		

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
e cont...		*Sarcochilus olivaceus*	Orchidaceae	*eo*		*	*		
		Stenocarpus sinuatus	Proteaceae	*ts*		*	*		
f		*Austrosteenisia blackii*	Fabaceae	*c*	*		*		
16 species		*Cordyline congesta*	Laxmanniaceae	*sh*	*		*		
		Cryptocarya bidwillii	Lauraceae	*ts*	*		*		
		Gossia bidwillii	Myrtaceae	*t*	*		*		
		Hodgkinsonia ovatiflora	Rubiaceae	*t*	*		*		
		Myrsine subsessilis subsp. *subsessilis*	Myrsinaceae	*ts*	*		*		
	*	*Cinnamomum oliveri*	Lauraceae	*ts*			*		
	*	*Clematis glycinoides*	Ranunculaceae	*c*			*		
	*	*Claoxylon australe*	Euphorbiaceae	*ts*			*		
	*	*Marsdenia flavescens*	Apocynaceae	*c*			*		
	*	*Pararchidendron pruinosum*	Mimosaceae	*ts*			*		
	*	*Plectorrhiza tridentata*	Orchidaceae	*eo*			*		
	*	*#Passiflora edulis*	Passifloraceae	*c*			*		
	*	*Parsonsia rotata*	Apocynaceae	*c*			*		
	*	*Rhysotoechia bifoliolata* subsp. *bifoliolata*	Sapindaceae	*ts*			*		
	*	*Symplocos thwaitesii*	Symplocaceae	*ts*			*		
g		*Acronychia pauciflora*	Rutaceae	*t*	*	*			
16 species		*Alpinia caerulea*	Zingiberaceae	*h*	*	*			
		Aphananthe philippinensis	Ulmaceae	*t*	*	*			
		Bonchardatia neurococca	Rutaceae	*t*	*	*			
		Beilschmiedia obtusifolia	Lauraceae	*t*	*	*			
		Callerya megasperma	Fabaceae	*c*	*	*			
		Davallia pyxidata	Davalliaceae	*ef*	*	*			
		Dockrillia bowmanii	Orchidaceae	*eo*	*	*			
		Elattostachys bidwillii	Sapindaceae	*t*	*	*			
		Gossia hillii	Myrtaceae	*t*	*	*			
		Flindersia australis	Rutaceae	*t*	*	*			
		Jagera pseudorhus var. *pseudorhus*	Sapindaceae	*ts*	*	*			
		Mallotus philippensis	Euphorbiaceae	*t*	*	*			
		Psychotria loniceroides	Rubiaceae	*ts*	*	*			
		Polyscias elegans	Araliaceae	*t*	*	*			

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres) 300	500	700	900	1100
g cont...		*Rhodosphaera rhodanthema*	Anacardiaceae	*t*	*	*			
h 19 species		*Beilschmiedia elliptica*	Lauraceae	*t*		*			
		Neoachmandra cunninghamii	Cucurbitaceae	*c*		*			
		Cassia marksiana	Caesalpiniaceae	*ts*		*			
		Cayratia eurynema	Vitaceae	*c*		*			
		Urtica incisa	Urticaceae	*h*		*			
		Cordyline petiolaris	Laxmanniaceae	*sh*		*			
		Dockrillia schoenina	Orchidaceae	*eo*		*			
		Gossia acmenoides	Myrtaceae	*t*		*			
		Gmelina leichhardtii	Lamiaceae	*t*		*			
		Enroschinus falcatus	Anacardiaceae	*ts*		*			
		Homalanthus nutans	Euphorbiaceae	*ts*		*			
		Maclura cochinchinensis	Moraceae	*c*		*			
		Legnephora moorei	Menispermaceae	*c*		*			
		Parsonsia ventricosa	Apocynaceae	*c*		*			
		Parsonsia velutina	Apocynaceae	*c*		*			
		Pteris umbrosa	Pteridaceae	*f*		*			
		Syzygium australe	Myrtaceae	*ts*		*			
		Stephania japonica var. *discolor*	Menispermaceae	*c*		*			
		Sicyos australis	Cucurbitaceae	*c*		*			
i 19 species		*Acmena smithii*	Myrtaceae	*t*				*	*
		Atractocarpus benthamianus subsp. *glaber*	Rubiaceae	*t*				*	*
		Caldcluvia paniculosa	Cunoniaceae	*t*				*	*
		Cyathea leichhardtiana	Cyatheaceae	*tf*				*	*
		Cupaniopsis flagelliformis var. *australis*	Sapindaceae	*t*				*	*
		Endiandra crassiflora	Lauraceae	*t*				*	*
		Doryphora sassafras	Atherospermaceae	*t*				*	*
		Geissois benthamii	Cunoniaceae	*t*				*	*
		Fieldia australis	Gesneriaceae	*e*				*	*
		Lenwebbia prominens	Myrtaceae	*t*				*	*
		Parsonsia fulva	Apocynaceae	*c*				*	*
		Pararistolochia laleyana	Aristolochiaceae	*c*				*	*
		Pandorea baileyana	Bignoniaceae	*c*				*	*

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
i cont...		*Palmeria scandens*	Monimiaceae	*c*				*	*
		Pilidiostigma glabrum	Myrtaceae	*sh*				*	*
		Orites excelsus	Proteaceae	*t*				*	*
		Rubus nebulosus	Rosaceae	*c*				*	*
		Quintinia verdonii	Quintiniaceae	*t*				*	*
		Syzygium crebrinerve	Myrtaceae	*t*				*	*
j 16 species		*Acradenia euodiiformis*	Rutaceae	*t*				*	
		Tasmannia insipida	Winteraceae	*sh*				*	
		Acronychia suberosa	Rutaceae	*t*				*	
		Acronychia pubescens	Rutaceae	*t*				*	
		Cephalomanes candatum	Hymenophyllaceae	*ef*				*	
		Cupaniopsis baileyana	Sapindaceae	*ts*				*	
		Dianella caerulea	Hemerocallidaceae	*h*				*	
		Duboisia myoporoides	Solanaceae	*ts*				*	
		Halfordia kendack	Rutaceae	*t*				*	
		Lastreopsis sp. 1	Dryopteridaceae	*f*				*	
		Pittosporum undulatum	Pittosporaceae	*ts*				*	
		Sarcopetalum harveyanum	Menispermaceae	*c*				*	
		Sarcochilus falcatus	Orchidaceae	*eo*				*	
		Synoum glandulosum subsp. *glandulosum*	Meliaceae	*t*				*	
		Streptothamnus moorei	Berberidopsidaceae	*c*				*	
		Stenocarpus salignus	Proteaceae	*ts*				*	
k 38 species		*Actephila lindleyi*	Phyllanthaceae	*t*	*	*	*		
		Vitex lignum-vitae	Lamiaceae	*t*	*	*	*		
		Trichosanthes subvelutina	Cucurbitaceae	*c*	*	*	*		
		Tetrastigma nitens	Vitaceae	*c*	*	*	*		
		Alectryon subcinereus	Sapindaceae	*t*	*	*	*		
		Adiantum formosum	Adiantaceae	*f*	*	*	*		
		Arytera divaricata	Sapindaceae	*t*	*	*	*		
		Arytera distylis	Sapindaceae	*t*	*	*	*		
		Brachychiton discolor	Sterculiaceae	*t*	*	*	*		
		Atalaya multiflora	Sapindaceae	*t*	*	*	*		
		Casearia multinervosa	Flacourtiaceae	*t*	*	*	*		

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres) 300	500	700	900	1100
k cont...		*Capparis arborea*	Capparaceae	*t*	*	*	*		
		Croton verreauxii	Euphorbiaceae	*t*	*	*	*		
		Clematis fawcettii	Ranunculaceae	*c*	*	*	*		
		Cleistanthus cunninghamii	Euphorbiaceae	*t*	*	*	*		
		Citrus australasica	Rutaceae	*t*	*	*	*		
		Cissus antarctica	Vitaceae	*c*	*	*	*		
		Cyperus tetraphyllus	Cyperaceae	*h*	*	*	*		
		Cryptocarya triplinervis var. *pubens*	Lauraceae	*t*	*	*	*		
		Dioscorea transversa	Dioscoreaceae	*c*	*	*	*		
		Dendrobium tetragonum	Orchidaceae	*eo*	*	*	*		
		Dendrobium speciosum	Orchidaceae	*eo*	*	*	*		
		Dendrocnide photinophylla	Urticaceae	*t*	*	*	*		
		Drypetes deplanchei	Putranjivaceae	*t*	*	*	*		
		Harpullia hillii	Sapindaceae	*t*	*	*	*		
		Lophostemon confertus	Myrtaceae	*t*	*	*	*		
		Lastreopsis munita	Dryopteridaceae	*f*	*	*	*		
		Melodorum leichhardtii	Annonaceae	*c*	*	*	*		
		Melodinus acutiflorus	Apocynaceae	*c*	*	*	*		
		Pandorea jasminoides	Bignoniaceae	*c*	*	*	*		
		Oplismenus imbecillis	Poaceae	*h*	*	*	*		
		Platycerium superbum	Polypodiaceae	*ef*	*	*	*		
		Planchonella myrsinifolia	Sapotaceae	*t*	*	*	*		
		Planchonella australis	Sapotaceae	*t*	*	*	*		
		Ripogonum brevifolium	Ripogonaceae	*c*	*	*	*		
		Streblus brunonianus	Moraceae	*t*	*	*	*		
		Solanum shirleyanum	Solanaceae	*sh*	*	*	*		
		Solanum serpens	Solanaceae	*sh*	*	*	*		
1 28 species	*	*Acronychia octandra*	Rutaceae	*t*					*
	*	*Arthropteris beckleri*	Nephrolepidaceae	*ef*					*
	*	*Blechnum wattsii*	Blechnaceae	*f*					*
	*	*Blechnum patersonii*	Blechnaceae	*f*					*
	*	*Berberidopsis beckleri*	Berberidopsidaceae	*c*					*
	*	*Callicoma serratifolia*	Cunoniaceae	*t*					*

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
1 cont...	*	*Dendrobium falcorostrum*	Orchidaceae	*eo*					*
	*	*Cyperus disjunctus*	Cyperaceae	*h*					*
	*	*Cyathea australis*	Cyatheaceae	*tf*					*
	*	*Cryptocarya foveolata*	Lauraceae	*t*					*
	*	*Dockrillia pugioniformis*	Orchidaceae	*eo*					*
	*	*Drymophila moorei*	Luzuriagaceae	*h*					*
	*	*Grammitis* sp.	Grammitidaceae	*ef*					*
	*	*Lastreopsis* sp.3	Dryopteridaceae	*f*					*
	*	*Hymenophyllum* sp.	Hymenophyllaceae	*ef*					*
	*	*Hibbertia scandens*	Dilleniaceae	*c*					*
	*	*Helmholtzia glaberrima*	Philydraceae	*h*					*
	*	*Marsdenia rostrata*	Apocynaceae	*c*					*
	*	*Lastreopsis* sp.2	Dryopteridaceae	*f*					*
	*	*Melicope hayesii*	Rutaceae	*ts*					*
	*	*Parsonsia iudnplicata*	Apocynaceae	*c*					*
	*	*Nothofagus moorei*	Nothofagaceae	*t*					*
	*	*Pennantia cunninghamii*	Pennantiaceae	*t*					*
	*	*Parsonsia tenuis*	Apocynaceae	*c*					*
	*	*Polyosma cunninghamii*	Escalloniaceae	*t*					*
	*	*Ripogonum fawcettianum*	Ripogonaceae	*c*					*
	*	*Ripogonum discolor*	Ripogonaceae	*c*					*
	*	*Quintinia sieberi*	Quintiniaceae	*t*					*
		Species richness			135	147	138	108	80

LITERATURE CITED

Adam, P. 1987. *New South Wales rainforests, the nomination for the world heritage list.* (NSW National Parks and Wildlife Service: Sydney).

Baur, G.N. 1964. *The future of rainforest in NSW, Forestry Commission of NSW Technical paper 5.* (Forestry Commissions of NSW: Sydney).

Beckmann, G.G. & Thompson, C.H. 1976. The soils. Pp 7-10. *In,* Monroe, R. & Stevens, N.C. (eds) *The Border Ranges, a land use conflict in regional perspective.* (The Royal Society of Queensland: Brisbane).

Belbin, L., Griffith University & The University of Queensland. 2003. *PATN: Pattern Analysis Package, Version 2.25.* (Griffith University & The University of Queensland: Brisbane).

Bostock, P.D. & Holland, A.E. 2007. *Census of the Queensland Flora 2007.* (Queensland Herbarium, Environmental Protection Agency: Brisbane).

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**: 325-349.

Cai, W., Crimp, S., Jones, R., McInnes, K., Durak, P., Cechet, B., Bathols, J. & Wilkinson, S. 2005. *Climate change in Queensland under enhanced*

greenhouse conditions: Report 2004-2005. (CSIRO: Aspendale).

Cornwall, C., Horiuchi, A. & Lehman, C. 2009. NOAA ESRL solar position calculator. (U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Earth System Research Laboratory, Boulder, Colorado). http://www.srrb.noaa.gov/highlights/sunrise/axel.html. Accessed 29/9/09.

Dolman, G.S. 1982. *Environmental parameters controlling the distribution of Nothofagus moorei*. Honours Thesis, University of New South Wales, Sydney.

Fisher, H.J. & Timms, B.V. 1978. Ferns of the rainforests of the Liverpool ranges. *Hunter Natural History* 10(4): 174-185.

Floyd, A.G. 2008. *Rainforest trees of mainland south-eastern Australia*. (Terania Rainforest Publishing: Lismore).

1990a. *Australian Rainforests in New South Wales Volume 1*. (Surrey Beatty & Sons Pty Ltd: Chipping Norton).

1990b. *Australian Rainforests in New South Wales Volume 2*. (Surrey Beatty & Sons Pty Ltd: Chipping Norton).

Fraser, L. & Vickery, J.W. 1939. The ecology of the upper Williams River and Barrington Tops Districts III. The Eucalypt forests and general discussion. *Proceedings of the Linnean Society of New South Wales* 64: 1-33.

Graham, B.W. 2001. *Tweed Volcanic Region: 360 million years ago to the present day*. (B.W. Graham: Tweed Heads).

Hopkins, M.S., Kikkawa, J., Graham, A.W., Tracey, J.G. & Webb, L.J. 1976. An ecological basis for the management of rain forest. Pp. 57-66. *In*, Monroe, R. & Stevens, N.C. (eds) *The Border Ranges, a land use conflict in regional perspective*. (The Royal Society of Queensland: Brisbane).

Houlder, D., Hutchinson, M.F., Nix, H.A. & McMahon, J.P. 2000. *ANUCLIM 5.1*. (Centre for Resource and Environmental Studies, The Australian National University: Canberra).

Hutley, L.B., Doley, D., Yates, D.J. & Boonsaner, A. 1997. Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany* 45: 311-329.

King, S. 1980. *The distribution, floristics and ecology of dry rainforests in the Macleay River gorges*. Honours Thesis, University of New England, Armidale.

Laidlaw, M.J., Olsen, M., Kitching, R.L. & Greenway, M. 2000. Tree floristic and structural characteristics of one hectare of subtropical rainforest in Lamington National Park, Queensland. *Proceedings of the Royal Society of Queensland* 109: 91-105.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J., Putland, D.A. & Kitching, R.L. 2011. The potential impacts of climate change on Australian subtropical rainforest. *Australian Journal of Botany* 59(5): 440-449.

Larcher, W. 1980. *Physiological Plant Ecology*. (Springer-Verlag: New York).

McDonald, W.J.F. 2010. The Tweed Shield Volcano Group. Pp. 39-50. *In*, Kitching, R.L, Braithwaite, R. & Cavanaugh, J. (eds), *Remnants of Gondwana: A natural and social history of the Gondwana rainforests of Australia*. (Surrey Beatty: Sydney).

McDonald, W.J.F. & Whiteman, W.F. 1979. *Moreton region vegetation map series: explanatory booklet for the Murwillumbah sheet*. (Botany Branch Qld Department of Primary Industries: Brisbane).

McKenzie, N., Jacquier, D., Isbell, R. & Brown, K. 2004. *Australian soils and landscapes: an illustrated compendium*. (CSIRO: Collingwood).

Olsen, M.F. & Lamb, D. 1984. Recovery of subtropical rainforest following storm damage. *Proceedings of the Ecological Society of Australia* 15: 297-301.

Rayment, G.E. & Higginson, F.R. 1992. *Australian laboratory handbook of soil and water chemical methods*. (Inkata Press: Melbourne).

Sattler, P. & Williams, R. 1999. *The conservation status of Queensland's bioregional ecosystems*. (Environmental Protection Agency: Brisbane).

Stevens, N.C. 1976. Geology and Landforms. Pp. 1-6. *In*, Monroe, R. & Stevens, N.C. (eds) *The Border Ranges, a land use conflict in regional perspective*. (The Royal Society of Queensland: Brisbane).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum -Nature* 55(2): 251-270.

Tang, Y. 2008. *Maintenance and dynamics of rainforest edges*. PhD Thesis, Griffith University, Brisbane.

Turner, J.C. 1976. An altitudinal transect in rain forest in the Barrington Tops area, New South Wales. *Australian Journal of Ecology* 1: 155-174.

Webb, L.J. 1978. A general classification of Australian rainforests. *Australian Plants* 9: 349–363.

Webb, L.J. 1969. Edaphic differentiation of some forest types in eastern Australia. II. Soil chemical factors. *Journal of Ecology* 57: 817-830.

Webb, L.J. 1968. Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology* 49(2): 296-311.

Webb, L.J. 1964. An historical interpretation of the grass balds of the Bunya Mountains, South Queensland. *Ecology* 45: 195-162.

Webb, L.J. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology* 47: 551-570.

Webb, L.J., Tracey, J.G. & Jessup, L.W. 1986. Recent evidence for autochthony of Australian tropical and subtropical rainforest floristic elements. *Telopea* 2(6): 575-589.

Willmott, W. 1992. *Rocks and landscapes of the Gold Coast hinterland.* (Geological Society of Australia, Queensland Division: Brisbane).

Limited surrogacy between predatory arthropods along an altitudinal gradient in subtropical rainforest

Kyran M. STAUNTON[1]

Christine S. FELLOWS[2] †

Roger L. KITCHING[1]

Akihiro NAKAMURA[1, 3]

Chris J. BURWELL[1, 3]

Robert J. RAVEN[3]

1. Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111 Australia. Email: staunton.k@gmail.com

2. Australian Rivers Institute and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. † Deceased.

3. Queensland Museum, South Brisbane Qld 4101, Australia.

Citation: Staunton, K.M., Fellows, C.S., Kitching, R.L., Nakamura, A., Burwell, C.J., & Raven, R.J. 2011 12 20: Limited surrogacy between predatory arthropods along an altitudinal gradient in subtropical rainforest. *Memoirs of the Queensland Museum – Nature* 55(2): 291-302. Brisbane. ISSN 0079-8835.

ABSTRACT

Biodiversity surveys are often forced to regard single taxa as surrogates for other groups within the same guild. Recently, concerns regarding impacts of climate change have driven a large body of research involving assemblage changes across elevational gradients. Such gradients have commonly been used to investigate changes within invertebrate assemblages, however, surrogacy of patterns displayed between taxa are rarely tested. Without sufficient testing of surrogacy among invertebrate groups, the impacts of described patterns in an ecosystem context, and their implications for biodiversity, remain either unknown or misinterpreted. To address this issue, we investigated changes in the communities of three different groups of predatory epigaeic arthropods, ants, predatory beetles and spiders, along an altitudinal gradient in subtropical rainforest in south-eastern Queensland, Australia. Predatory arthropods were sampled with pitfall traps at four replicate plots at each of five elevations; 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). The three groups displayed differential responses to altitude. Ants responded most clearly with a decline in species richness and progressive change in composition with increasing altitude with depauperate fauna at the highest elevation. Beetles were abundant and species rich throughout the gradient although they were most speciose at 900 m a.s.l. Beetle assemblages progressively changed from low to high elevations, but assemblages at the highest elevation were distinct due to numerous species restricted to this altitude. The abundance and species richness of spiders were similar throughout the gradient, but spiders were distinctly separated into low (300-700 m a.s.l.) and high (900-1100 m a.s.l.) altitude assemblages. Our results indicate that predictions about the impacts of climate change on ecosystem processes such as predation will vary, especially at the highest elevations, according to taxonomic group sampled.

INTRODUCTION

Elevational gradients are characterised by predictable changes in local climatic variables such as temperature, precipitation and humidity (Barry 1992), which make them ideal for investigating the impacts of climate change upon assemblages of species (Richardson *et al.* 2005; Botes *et al.* 2006; Shoo *et al.* 2006). Distributions of organisms are strongly influenced by detectable climatic niches or envelopes (Bakkenes *et al.* 2002; Araujo *et al.* 2004, 2005; Bomhard *et al.* 2005). In montane ecosystems, changes in altitude significantly affect climatic niches and in turn species' distributions and community composition (Walther *et al.* 2002). In habitats such as rainforest, which contain extremely diverse invertebrate fauna, species turnover across elevational gradients can be substantial with unique fauna found at higher elevations (Fisher 1998; Bruhl *et al.* 1999).

Rainforest invertebrates exhibit very high abundance and diversity, occupying a large range of microhabitats and ecological niches (Stork 1993). As a result, they are known to play essential roles in many ecological processes including predation, pollination, herbivory and soil decomposition (Speight *et al.* 1999). Ecological studies often categorise invertebrates into various trophic levels or guilds as a means of relating their relevance to ecosystem functioning (e.g. Hammond 1990; Andrew & Hughes 2004; Gray *et al.* 2007; Grimbacher & Stork 2007). Invertebrates belonging to different trophic levels have already been demonstrated to exhibit varied sensitivities to climatic factors (Voigt *et al.* 2003), however, there has been little subsequent research into the potential impacts of climate change on invertebrate trophic groups. Whilst solid frameworks exist regarding general mechanisms driving certain changes in herbivorous assemblages within rainforest environments, much work is still required regarding predatory invertebrates (Kitching 2006). Insight regarding climate change impacts on predatory rainforest invertebrates can be gathered through assessing changes in predatory assemblages within elevational gradients.

Assemblages of predatory invertebrates have been sampled across elevational gradients in several studies (Olson 1994; Bruhl *et al.* 1999; Botes *et al.* 2006). Many such studies focus on particular invertebrate taxa such as ants (e.g. Fischer 1998), spiders (e.g. Chatzaki *et al.* 2005) or opiliones (Almeida-Neto *et al.* 2006). This single taxon approach is often adopted due to the taxonomic impediment associated with processing large catches of multiple invertebrate groups (Kotze & Samways 1999; Progar & Schowalter 2002). Studies of single taxa inevitably raise the question of surrogacy: to what extent can the patterns observed in one taxon be assumed in others? Clearly groups with limited surrogacy demonstrate trends that cannot be extrapolated to other taxa (Kotze & Samways 1999). Thus, it is imperative to not only understand assemblage patterns across elevational gradients but also the surrogacy of such patterns between similar taxa in similar habitats. In order to confidently identify the level of surrogacy between groups, simultaneous study of multiple taxa must be performed.

In this study a multi-taxa approach was used to assess patterns within predatory guilds across an elevational gradient. Three taxa were examined: Formicidae (ants), predatory Coleoptera (beetles) and Araneae (spiders). In order to determine the level of surrogacy displayed between these predatory groups, patterns of abundance, species richness, and compositional change were examined across an elevational gradient.

METHODS

Study site and sampling methods

This study was conducted as part of the IBISCA-Queensland Project (Kitching *et al.* 2011), which investigated the distributional patterns of a wide range of invertebrate groups along an elevational transect from approximately 300 to

1100 m above sea level (a.s.l.). This transect was established within continuous rainforest in the West Canungra Creek catchment of Lamington National Park, south-east Queensland, Australia (28°09'–28°16'S, 153°06'–153°11'E). The elevational gradient was subdivided into five levels of altitude (viz. 300, 500, 700, 900, 1100 m a.s.l.), each with four replicated plots within an elevational range of 90 m a.s.l. (see Kitching *et al.* 2011 for the precise altitudes of plots). All plots were located within rainforest but the structural type and floristic composition of the rainforest changes with altitude. Plots at 300 m a.s.l. were located within araucarian complex notophyll vine forest, those at 500 and 700 m a.s.l. in warm subtropical complex notophyll vine forest, those at 900 m a.s.l. in cool subtropical complex notophyll vine forest and those at 1100 m a.s.l. in microphyll fern forest with a canopy dominated by Antarctic beech (*Nothofagus moorei*) (Laidlaw *et. al.* 2011a). The IBISCA-Queensland transect also encompasses different climate and soil properties, which are summarised in Strong *et al.* (2011).

Each plot consisted of a 20 x 20 m quadrat. Plots within each altitude were separated by at least 400 m. Plots were established away from significant tree falls or light gaps, at least 50 m from permanent water sources, and did not have a known history of anthropogenic disturbance.

Within each quadrat, we installed nine pitfall traps in a 5 x 5 crossed array, with each trap separated by one metre. Each nine-trap array was considered as one sampling unit and was positioned within the quadrat using randomly created coordinates. Pitfall traps were polyethylene plastic vials, 50 mm in diameter and 150 mm in depth, placed within orange electrical conduit PVC sleeves and filled with 50 ml of a 70:30 ethanol/water solution. They were set flush with the ground and a square rain cover was suspended about 5 cm above each. Pitfall traps were left open for nine days and catches from all nine traps at each plot were pooled before analyses. The trapping methods are described in detail in Kitching *et al.* (2005).

We conducted pitfall trapping in October 2006 and February 2007, and catches from these two sampling occasions were combined before analyses. All spiders (Araneae), ants (Formicidae, only workers) and beetles (Coleoptera) were extracted from traps and sorted to species or morphospecies by CJB (ants), RJR (spiders) and KMS (beetles). In this study we considered all spider and ant species to be predatory and only beetles from families known to consist primarily of predatory taxa according to Lawrence & Britton (1991) were included in analyses. Voucher specimens were deposited in the Queensland Museum, Brisbane (ants and spiders) and the Arthropod Biodiversity Laboratory, Griffith University, Nathan, Queensland (beetles).

Data analysis

To investigate sampling sufficiency of the three arthropod groups, we first generated individual-based species accumulation curves using the expected richness function (Coleman curves) available from EstimateS software ver. 8.2 (Colwell 2009). Individual-based rarefaction curves represent expected species density, given n individuals. Species richness of local arthropod communities was also estimated using the Abundance-based Coverage Estimator (ACE) which estimates the number of species by taking unseen species (i.e. species not collected) into consideration.

To test for differences in species richness and total abundance of the three arthropod groups among different elevational zones, single-factor ANOVAs were performed with SPSS ver. 13.0 (SPSS Inc. 2004). For *post-hoc* pairwise comparisons we employed Tukey HSD tests. All abundance data were log-transformed before analyses.

To examine changes in the composition of arthropod assemblages across altitude, we used principal coordinates analysis (PCO) available in PERMANOVA+ (Anderson *et al.* 2008) to generate an ordination for each arthropod group. Instead of conventionally used

TABLE 1. Number of species and individuals of each genus (ants) and family (predatory beetles and spiders) of the three predatory arthropod groups sampled.

Ant genus	No. species	No. individuals
Amblyopone	1	1
Anonychomyrma	2	44
Camponotus	1	1
Carebara	2	28
Cerapachys	1	1
Colobostruma	1	1
Crematogaster	2	17
Discothyrea	1	1
Heteroponera	1	2
Hypoponera	2	9
Leptogenys	4	54
Leptomyrmex	2	6
Lordomyrma	1	1
Mayriella	3	11
Monomorium	7	42
Myrmecina	1	4
Notoncus	1	22
Notostigma	1	3
Pachycondyla	2	4
Paraparatrechina	1	1
Pheidole	7	685
Ponera	1	1
Prionopelta	1	5
Pristomyrmex	1	3
Prolasius	5	80
Pseudonotoncus	1	1
Rhopalothrix	1	1
Rhytidoponera	2	280
Solenopsis	1	250
Sphinctomyrmex	1	1
Strumigenys	2	2
Tapinoma	1	1
Technomyrmex	2	3
Total	63	**1566**

Beetle family	No. species	No. individuals
Carabidae	16	58
Coccinellidae	1	1
Scydmaenidae	11	28
Staphylinidae	82	1635
Total	**110**	**1722**

Spider family	No. species	No. individuals
Amaurobiidae	6	88
Amphinectidae	1	9
Anapidae	2	97
Barychelidae	1	13
Clubionidae	3	10
Cycloctenidae	7	156
Desidae	2	14
Dipluridae	1	2
Gnaphosidae	3	28
Gradungulidae	1	9
Hahniidae	1	1
Hexathelidae	1	1
Idiopidae	1	3
Lamponidae	3	10
Linyphiidae	9	61
Liocranidae	1	1
Lycosidae	7	90
Malkaridae	1	14
Micropholcommatidae	2	3
Mimetidae	1	1
Mysmenidae	1	66
Nemesiidae	5	27
Nicodamidae	1	2
Oonopidae	6	62
Orsolobidae	1	12
Pisauridae	1	2
Salticidae	10	33
Sparassidae	4	22

TABLE 1. cont...

Spider family	No. species	No. individuals
Stiphidiidae	2	3
Tengellidae	2	7
Textricellidae	1	1
Theridiidae	6	28
Theridiosomatidae	1	2
Thomisidae	1	11
Trochanteriidae	2	3
Zodariidae	3	27
Zoridae	2	49
Zoropsidae	2	4
Total	**105**	**972**

TABLE 2. *F* and *P* values of the effect of elevational differences on the total abundance, species richness and assemblage composition of the three predatory arthropod groups. Parametric ANOVA was conducted on total abundance and species richness, whereas permutational multivariate ANOVA (PERMANOVA) was conducted on assemblage composition. Significant *P* values are shown in bold.

	F (pseudo-F)	*P*
Total abundance		
Ants	22.12	**<0.001**
Predatory beetles	2.07	0.137
Spiders	1.75	0.192
Species richness		
Ants	21.61	**<0.001**
Predatory beetles	5.24	**0.008**
Spiders	3.12	**0.047**
Assemblage composition		
Ants	4.63	**<0.001**
Predatory beetles	3.37	**<0.001**
Spiders	3.21	**<0.001**

non-metric multidimensional scaling (NMDS) ordination, we used PCO because the scales of the resulting PCO axes are interpretable in the units of the resemblance measure (Anderson *et al.* 2008). Primary and secondary axes (which generally explain a large proportion of the variation in assemblage composition) were used to generate two-dimensional ordinations. Primary axis values were also plotted against the actual altitudes of the sampled plots to compare how assemblage composition changed with increasing altitude among the three arthropod groups. Abundance data were square-root transformed prior to analyses and the Bray-Curtis index was used to quantify similarities in assemblage composition between samples. Due to the extremely low abundance of ants at one of the 1100 m plots (1% of the total ant abundance) it was removed from the multivariate analyses of ant assemblages. We tested the influence of altitude on assemblage composition using PERMANOVA (permutational multivariate analysis of variance) available in PERMANOVA+ (Anderson *et al.* 2008). PERMANOVA calculates *F* statistics (pseudo-*F*) based on a chosen distance measure of assemblage composition (Bray-Curtis index here), and obtains *P* values using permutation techniques (4999 unrestricted permutations of raw data). Altitude was incorporated in the analyses as a fixed factor and Type III Sums of Squares was used to calculate pseudo-*F* statistics.

RESULTS

Overall composition

The predatory guild comprised of ants, predatory beetles and spiders was represented by a total of 4260 individuals (Table 1). Ants, 1566 specimens of 63 species, accounted for 37% of the total individuals. Ants were dominated by the genus *Pheidole*, which consisted of seven morphospecies and accounted for 44% of the total ant abundance. Predatory beetles consisted of 1722 individuals (40% of all predators) and 110 species. Staphylininae comprised the largest proportion of the predatory beetles (Table 1). Spiders were represented by 972 individuals (23% of all predators) from 105 species. The single species of Cycloctenidae (*Cycloburra* ibi9) was the

most abundant species contributing 13% to the total spider abundance.

Individual-based species accumulation curves for ants and spiders showed gradual abatement in the incline of the slopes towards the end of the curves (Fig. 1). This, however, was not the case for predatory beetles with the species accumulation curve still sharply increasing. Accordingly, there were smaller differences between estimated (ACE) and observed species richness for ants (estimated = 91 species versus observed = 63) and spiders (138 vs 105), whereas more than twice as many species were estimated than observed for predatory beetles (258 vs 110).

Elevational patterns

Total abundances of all three arthropod groups did not vary greatly between elevational zones, with the exception of 1100 m a.s.l., where ant abundance declined sharply and significantly (Fig. 2; Table 2). Unlike total abundances, species richness of all three arthropod groups was significantly influenced by altitude (Table 2). Post-hoc tests showed a gradual decline in ant species richness with increasing altitude (Fig. 2). Beetle species richness significantly peaked at mid-elevations with greater species richness at 700 and 900 m a.s.l. Due to a marginally significant ($P = 0.047$) effect of altitude on spider species richness, none of the pair-wise comparisons were significantly different (Fig. 2).

All three arthropod groups progressively changed assemblage compositions from 300 to 1100 m a.s.l. (Fig. 3). The results of PERMANOVA concurred with these observed patterns, showing a highly significant effect of altitude on the assemblage composition of all three predatory groups. The fine scale patterns of their responses to altitude were, however, different (Fig. 4). Ants displayed an almost linear relationship between the primary PCO axis values and altitude. Primary PCO values of beetles gradually declined from 300 to 900 m a.s.l. and then sharply dropped at 1100 m a.s.l. In contrast, spiders did not exhibit clear elevational patterns at lower elevations but there was a prominent discrepancy in primary PCO values between lower (300-700 m a.s.l.) and higher (900, 1100 m a.s.l.) altitudes.

DISCUSSION

The steep slope at the end of predatory beetle species accumulation curve, reinforced by the estimated beetle species richness at more than double the observed richness, suggests that this arthropod group was substantially under-sampled in our study. This is attributable to the fact that most beetle species were represented by singletons and doubletons (76 of a total of 110 species, 69%) with few common species (13 species represented by more than 10 individuals). Ants and spiders appeared to be more adequately sampled, although estimated species-richness was 44% and 29% higher than observed richness respectively. Despite potential under-sampling, assemblage composition of all three predator taxa responded clearly to changes in altitude. Although increased sampling intensity may have yielded more species, we believe that the overall patterns of predatory taxa would not differ substantially from those we observed in this study.

Of the three arthropod groups sampled, ants responded most strongly to altitude. Although the abundance of ants was more or less similar across most of the gradient, there was a sharp and significant reduction in ant abundance at the highest elevation. Ant species richness and assemblage composition changed across the entire gradient, with a decline in richness (Fig. 2) and progressive change in ant assemblages (Figs 3, 4) from low to mid to high altitudes. These results mirror those of other studies on ants along the IBISCA-Queensland transect (Burwell & Nakamura 2009, 2011). Burwell and Nakamura, who sampled ants more intensively, targeting ground, litter and arboreal habitats, also found markedly less ants at 1100 m a.s.l., and a gradual decline of species richness and progressive changes in assemblage composition

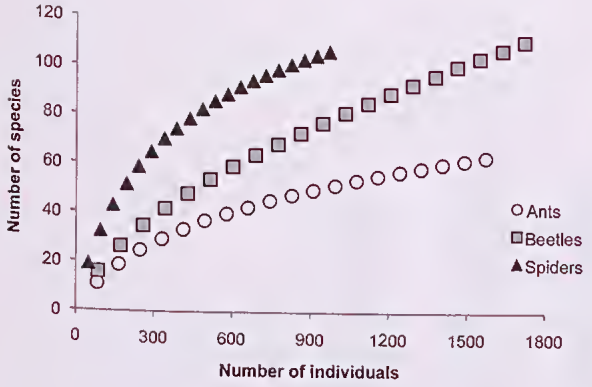


FIG. 1. Individual-based species accumulation curves of ants, predatory beetles and spiders collected in pitfall traps from the IBISCA-Queensland transect in Lamington National Park.

with increasing altitude. In addition, Bito *et al.* (2011) found significant decline in ant predation pressure at ground-level, measured as the proportion of tuna baits occupied by ants, along the IBISCA-Queensland transect. Similar declines in ant species richness and abundance with increasing altitude have been documented elsewhere (Olson 1994; Bruhl *et al.* 1999). Hodkinson (2005) suggested that ants, in general, are characterised by depauperate assemblages at higher elevations.

Ants are known to be sensitive to changes in climatic conditions (Sanders *et al.* 2007). Indeed, the observed responses of ants in our study were consistent with changes in climatic conditions measured along the IBISCA-Queensland gradient. Gradual changes in ant species richness and assemblage composition paralleled gradual decline of median temperature with increasing altitude (Strong *et al.* 2011). In addition, rainfall is higher at higher elevations in the region (Strong *et al.* 2011) and areas above around 900 m a.s.l. receive additional moisture inputs via cloud-stripping (Laidlaw *et al.* 2011b). Consequently soil moisture increases with increasing elevation, and at 1100 m a.s.l. high soil moisture is maintained throughout the year (Strong *et al.* 2011). Low temperatures at high elevations combined with reduced insolation associated with increased cloud cover (Rahbek 1995) have been suggested to reduce foraging time for ants and slow their developmental rates (Fisher 1998). High soil and litter moisture levels at high elevations have also been suggested to reduce the availability of nest sites, and to interfere with the foraging activity of small ants (Bruhl *et al.* 1999). Thus the colder and, particularly, the wetter conditions at the highest altitude most probably account for its depauperate ant fauna.

Predatory beetles showed a mid-altitudinal peak in species richness, and both species richness and abundance at the highest elevation (1100 m a.s.l.) were comparable to those found at lower elevations. Assemblage composition of predatory beetles progressively changed from low to mid-elevations, but those found at 1100 m were dramatically different from lower elevations. Unlike ants that had very depauperate assemblages at the highest elevation, beetles at this elevation were characterised by many species unique to this particular elevation (12 species). Although our results need to be interpreted carefully due to possible undersampling, the observed patterns were consistent with those found by Ødegaard and Diserud (2011) who conducted more extensive surveys of beetles in the understorey vegetation within the same survey plots.

In contrast to ants and beetles, both the species richness and abundance of spiders were only weakly related to altitude. Altitudinal changes in spider assemblages were idiosyncratic with a clear separation between assemblages from lower (viz. 300, 500, 700 m a.s.l.) and higher (viz. 900, 1100 m) elevations. Unlike beetles, there were few high altitude specialists among the spiders; only four species were restricted to 1100 m a.s.l. An altitudinal study in rainforest in tropical Queensland found lower level of species turnover among spiders compared with beetles (Monteith & Davies 1991). Similarly, spiders exhibited

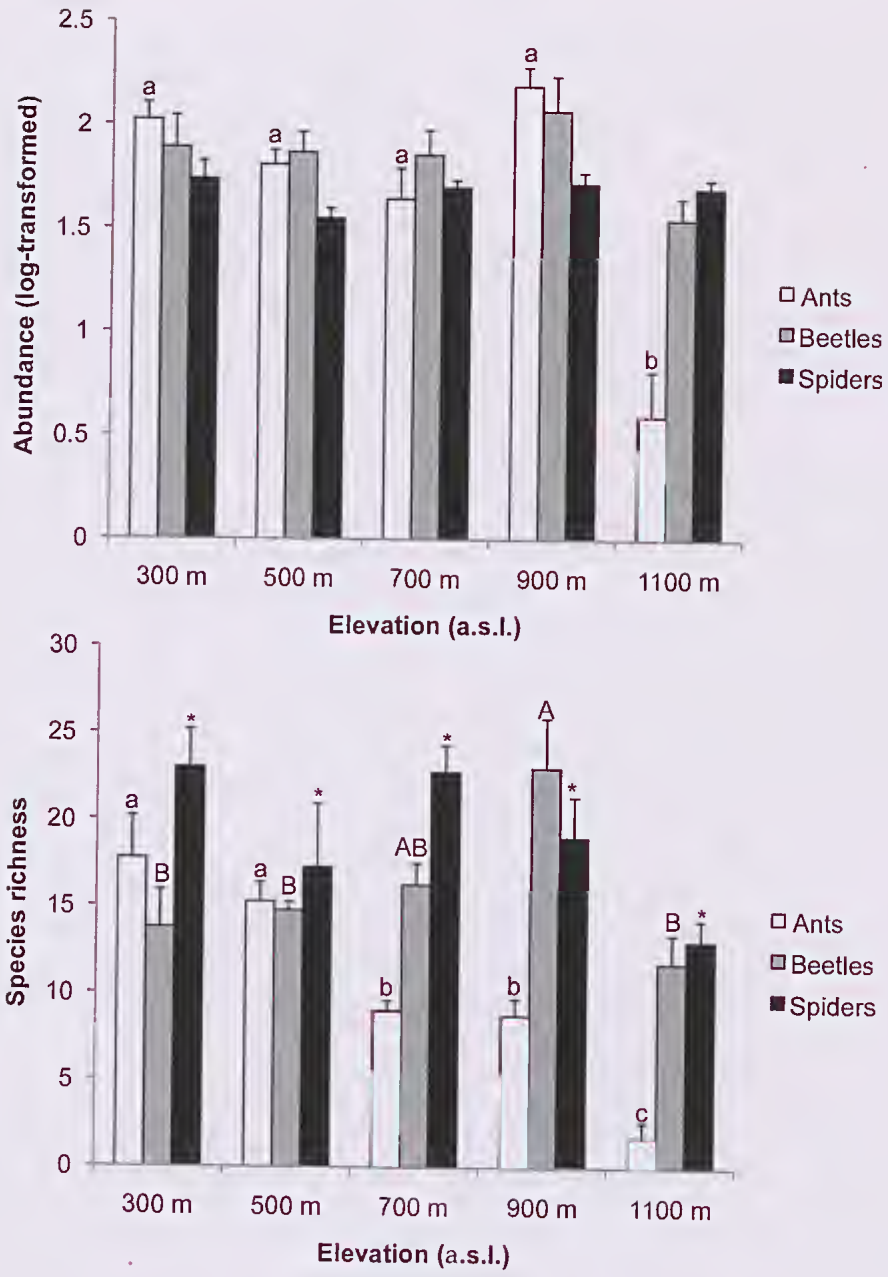


FIG. 2. Mean (+SE) total abundance (log-transformed) and species richness of ants, predatory beetles and spiders collected in pitfall traps across five elevational zones in Lamington National Park. Results of post-hoc pair-wise comparisons are shown using different letters to indicate significant differences between elevational zones. Lower case letters are for ants and upper case letters for predatory beetles. * Although the main factor was significant for spiders, none of the pair-wise comparisons displayed significant differences due to only a marginal effect of the main factor (P=0.047).

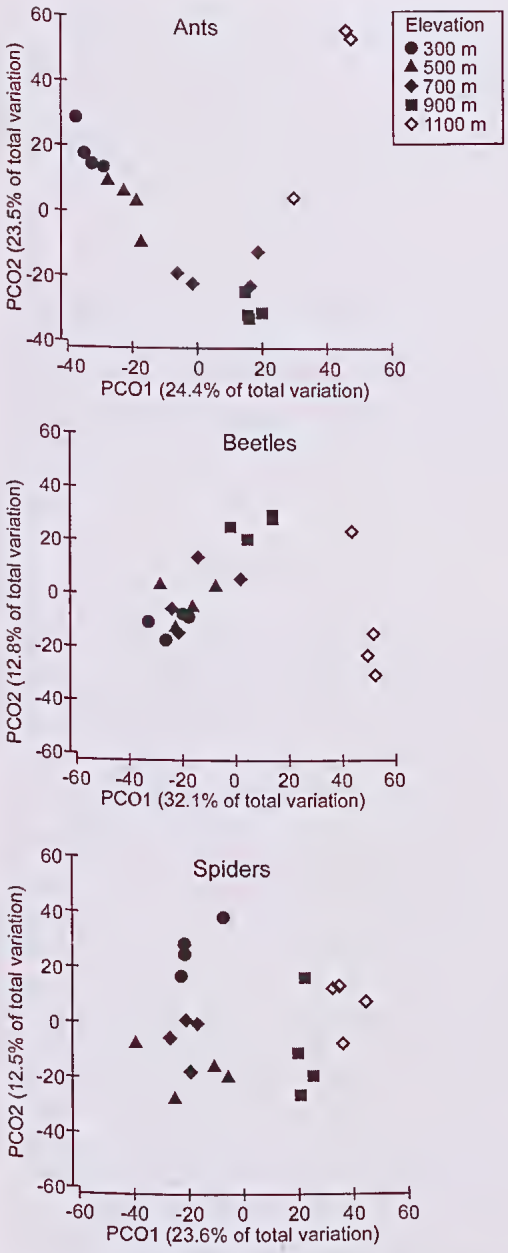


FIG. 3. PCO ordinations based on ant, predatory beetle and spider species assemblages (square-root transformed) across the five elevational zones, showing the primary and secondary axes values. Total variation of the assemblage composition explained by each axis is also displayed.

comparatively low species turnover among different forest types (Oliver & Beattie 1996b). Perhaps spiders are more tolerant to changes in habitat conditions, and in general spider species may display broader altitudinal ranges compared to ants and beetles.

Despite significant responses to altitude in the assemblage composition of all three taxa examined here, their response patterns were distinctive (Fig 3), suggesting limited surrogacy among these predatory arthropod groups. Studies attempting to assess the impacts of future climate change on ecological processes such as predation, must be mindful that predictions based on one taxonomic group may not apply to other groups. For example, consider potential changes in the predator landscape at the highest elevations of the IBISCA-Qld transect (1100 m a.s.l.) under moderate warming of about 1.5°C. With an increase in temperature of that magnitude, organisms would be predicted to shift their distributions upslope by around 200 m. If we first consider spiders, we would predict little change as spider abundance, richness and assemblage composition is currently similar at 900 and 1100 m a.s.l. For beetles, predation pressure may change little as overall abundances are currently similar at 900 and 1100 m a.s.l. However, the composition of predatory beetles may shift substantially, with the potential loss of many high altitude restricted species, but an overall increase in species richness as a greater number of species from 900 m a.s.l. move upslope. With regards to ants, a future scenario may be dramatically different, where the now depauperate ant fauna at 1100 m a.s.l. is replaced by a suite of additional species found at 900 m a.s.l., and most importantly overall ant abundance, and hence predation pressure, would be expected to increase dramatically.

These 'just-so' predictions are, however, oversimplifications and inter- and intra-guild interactions will complicate climate change impacts. Predatory beetles have been suggested to be susceptible to competition from ants (Darlington 1943; Reznikova & Dorosheva

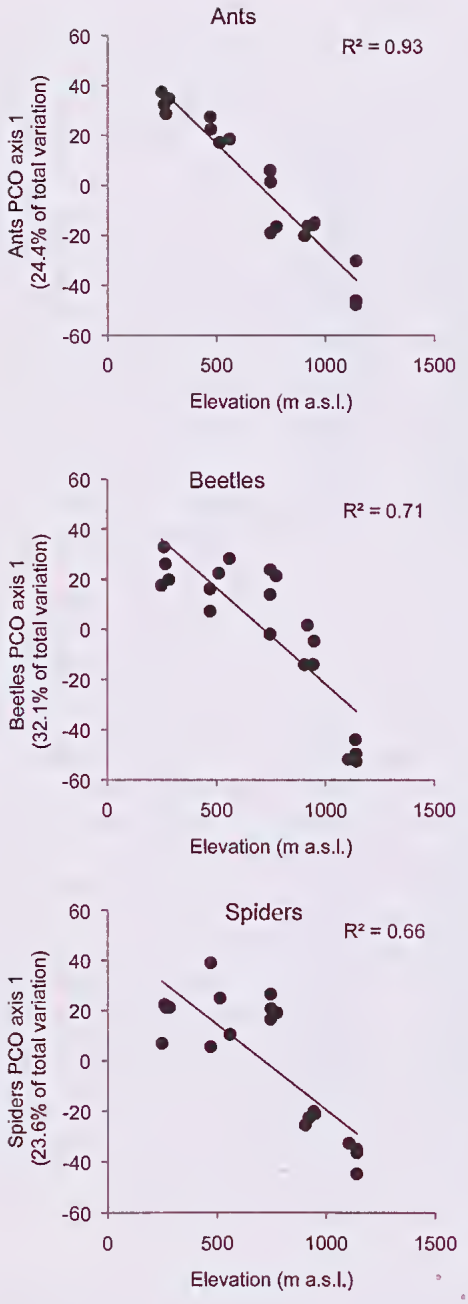


FIG. 4. Values of the primary PCO axis plotted against actual altitudes of the survey plots for ants, predatory beetles and spiders. A straight line was also fitted with the R^2 value for each arthropod group.

2004, Hawes *et al.* 2002). In high elevation rainforests abundant carabid populations have been attributed to a coincidental scarcity of ants (Darlington 1971; Olson 1994). Potential invasion of the highest elevations (primarily by ants) at Lamington National Park may consequently impact upon resident predators, particularly carabid beetles.

The observation that different predatory groups respond in contrasting fashions to climatic changes (as reflected by adjacent altitudes) underlines the need for the use of multiple taxa in biodiversity monitoring programmes. Such prescriptions may test the availability of financial and expert resources yet are clearly essential.

ACKNOWLEDGEMENTS

We thank the many IBISCA staff and volunteers without whom this research would not be possible and the Queensland National Parks and Wildlife Service for permission to conduct this study in Lamington National Park. Thanks also to Griffith University Centre for Innovation and Conservation Strategies (now the Environmental Futures Centre) who provided funding to KMS. This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort.

LITERATURE CITED

Almeida-Neto, M., Machado G., Pinto-da-Rocha, R., & Giaretta, A.A. 2006. Harvestman (Arachnida:

Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain rapoport's rule? *Journal of Biogeography* 33: 361-375.

Anderson M.J., Gorley R.N. & Clarke K.R. (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. (PRIMER-E: Plymouth, UK).

Andrew, N.R. & Hughes, L. 2004. Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change. *Ecological Entomology* 29: 527-542.

Araujo, M.B., Cabeza M., Thuiller, W., Hannah, L. & Williams, P.H. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10: 1618-1626.

Araujo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. 2005. Validation of species-climate impact models under climate change. *Global Change Biology* 11: 1504-1513.

Bakkenes, M., Alkemade J.R.M., Ihle, F., Leemans, R. & Latour, J.B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* 8: 390-407.

Barry, R.G. 1992. *Mountain Weather and Climate* (2nd ed.). (Routhledge: London/New York).

Bito, D., Novotny, V., Burwell, C.J., Nakamura, A., Kitching, R.L., Ødegaard, F. 2011. Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient. *Memoirs of the Queensland Museum-Nature* 55(2): 451-461.

Bomhard, B., Richardson, D.M., Donaldson, J.S., Hughes, G.O., Midgley, G.F., Raimondo, D.C., Rebelo, A.G., Rouget, M. & Thuiller, W. 2005. Potential impacts of future land use and climate change on the red list status of the Proteaceae in the Cape Floristic Region, South Africa. *Global Change Biology* 11: 1452-1468.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P., Chown, S.L. 2006. Ants, altitude and change in the northern cape floristic region. *Journal of Biogeography* 33: 71-90.

Bruhl, C.A., Mohamed, M. & Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15: 265-277.

Burwell, C.J. & Nakamura, A. 2009. Ants with altitude: the potential of ants as climate change bioindicators in subtropical rainforest. *News Bulletin of the Entomological Society of Queensland* 37: 130-138.

Burwell, C.J. & Nakamura, A. 2011. Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum-Nature* 55(2): 391-411.

Chatzaki, M., Lymberakis, P., Markakis, G. & Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography* 32: 813-831.

Colwell, R.K. 2009. EstimateS: Statisical estimation of species richness and shared species from samples. Version 8.2. User's Guide and Application. Published at: http://purl.oclc.org/estimates.

Darlington, P.J. 1943. Carabidae of mountains and islands: data on evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs* 13: 37-61.

1971. The carabid beetles of New Guinea. Part iv. General considerations; analysis and history of fauna; taxonomic supplement. *Bulletin of the Museum of Comparative Zoology* 142: 1-337.

Fisher, B.L. 1998. Ant diversity patterns along an elevational gradient in the Reserve Speciale d'Anjanahanbe-Sud and on the Western Masoala Peninsula, Madagascar. *Fieldiana Zoology* 90: 39-67.

Gray, M.A., Baldauf, S.L., Mayhew, P.J. & Hill, J.K. 2007. The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* 21: 133-141.

Grimbacher, P.S. & Stork, N.E. 2007. Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest. *Austral Ecology* 32: 77-85.

Hammond, P. 1990. Insect abundance and diversity in the Dumoga-Bone National Park N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. Pp. 197-247. *In*, Knight, W. & Holloway, J.D. (eds) *Insects and the rain forest of South East Asia (Wallacea)*. (The Royal Entomological Society of London: London).

Hawes, C., Stewart, A.J.A & Evans, H.F. 2002. The impact of wood ants (*Formica rufa*) on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in a scots pine plantation. *Oecologia* 131: 612-619.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80: 489-513.

Kitching, R.L. 2006. Crafting the pieces of the diversity jigsaw puzzle. *Science* **313**: 1055-1057.

Kitching, R.L., Boulter, S.L., Vickerman, G., Laidlaw, M., Hurley, K.L. & Grimbacher, P.S. 2005. *The Comparative Assessment of Arthropod and Tree Biodiversity in Old-World Rainforests. The Rainforest CRC / Earthwatch Protocol Manual*, 2 edn. (Cooperative Research Centre for Tropical Rainforest Ecology and Management).

Kitching, R.L., Putland, D.A., Ashton, L.A., Laidlaw, M.J., Boulter S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.

Kotze, D.J. & Samways, M.J. 1999. Support for the multi-taxa approach in biodiversity assessment, as shown by epigaeic invertebrates in an afromontane forest archipelago. *Journal of Insect Conservation* **3**: 125-143.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011a. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55**(2): 271-290.

Laidlaw, M.J., McDonald, W.J.F, Hunter, R.J., Putland, D.A. & Kitching, R.L. 2011b. The potential impacts of climate change on Australian subtropical rainforest. *Australian Journal of Botany* **59**: 440-447.

Lawrence, J.F. & Britton, E.B. 1991. Coleoptera. Pp. 543-683. *In*, Naumann, I.D. (ed), *The Insects of Australia*. (Melbourne University Press: Melbourne).

Monteith, G.B. & Davies, V.T. 1991. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical north Queensland. Pp. 354-362. *In*, Warren, G. & Kershaw, P. (eds) *The rainforest legacy: Australian national rainforest study*. Vol. 2 - flora and fauna. (Australian Government Publishing Service: Canberra).

Oliver, I. & Beattie, A.J. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* **10**: 99-109.

Olson, D. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* **10**: 129-150.

Ødegaard, F. & Diserud, O.H. 2011. Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park, (Queensland, Australia). *Memoirs of the Queensland Museum-Nature* **55**(2): 359-374.

Progar, R.A. & Schowalter, T.D. 2002. Canopy arthropod assemblages along a precipitation and latitudinal gradient among Douglas-fir *Pseudotsuga menziesii* forests in the Pacific Northwest of the United States. *Ecography* **25**: 129-138.

Rahbek, C. 1995. The elevational gradient of species richness - a uniform pattern. *Ecography* **18**: 200-205.

Reznikova, Z. & Dorosheva, H. 2004. Impacts of red wood ants *Formica polyctena* on the spatial distribution and behavioural patterns of ground beetles (Carabidae). *Pedobiologia* **48**: 15-21.

Richardson, B.A., Richardson, M.J. & Soto-Adames, F.N. 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Animal Ecology* **74**: 926-936.

Sanders, N.J., Lessard, J., Fitzpatrick, M.C. & Dunn, R.R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* **16**: 640-649.

Shoo, L.P., Williams, S.E. & Hero, J.M. 2006. Detecting climate change induced range shifts: where and how should we be looking? *Austral Ecology* **31**: 22-29.

Speight, M.R., Hunter, M.D. & Watt, A.D. 1999. *Ecology of insects: concepts and applications*. (Blackwell Science Ltd: London).

SPSS Inc. 2004. Spss for windows ver. 13.0. (SPSS Inc.: Chicago).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D.A. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Stork, N.E. 1993. How many species are there? *Biodiversity and Conservation* **2**: 215-232.

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bahrmann, R., Fabian, B., Heinrich, W., Kohler, G., Lichter, D., Marstaller, R. & Sander, F.W. 2003. Trophic levels are differentially sensitive to climate. *Ecology* **84**: 2444-2453.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389-395.

Assessing the abundance of seven major arthropod groups along an altitudinal gradient and across seasons in subtropical rainforest

Sarah L. BOULTER

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan 4111, Qld, Australia. Email: s.boulter@griffith.edu.au

Christine L. LAMBKIN

Noel T. STARICK

Biodiversity Program, Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia.

Citation: Boulter, S.L., Lambkin, C.L. & Starick, N.T. 2011 12 20: Assessing the abundance of seven major arthropod groups along an altitudinal gradient and across seasons in subtropical rainforest. *Memoirs of the Queensland Museum – Nature* 55(2): 303-313. ISSN 0079-8835.

ABSTRACT

Changes in the abundance of seven major arthropod taxa with changes in altitude and season were investigated in a subtropical rainforest using both Malaise traps and flight intercept traps. Sampling was conducted as part of the IBISCA-Queensland Project at four plots established at each of five altitudes (300, 500, 700, 900 and 1100 m above sea level) within continuous rainforest. Trapping was carried out at four times throughout a 12 month period, comprising a dry season (winter) sample and samples in the early (spring), mid (summer) and late (autumn) wet season. Clear seasonal changes in the abundance of arthropods sampled were evident as well as changes in community assemblages. The winter sample in particular was different to all other seasons. Limited response to altitude was detected, with the greatest differences between altitudes along the gradient found in summer and winter samples. The limited altitudinal trend is likely the result of the scale of sampling with individual species and families expected to show contrasting responses. The clear influence of season, however, does demonstrate the sensitivity of these broad arthropod groups to climate variability and cues. ❐ *IBISCA, arthropod, subtropical rainforests.*

Changes in environmental conditions associated with changes in altitude are well known and broadly predictable. As altitude increases, temperature and partial pressure of atmospheric gases will decrease; rainfall, UV radiation and wind speed can be expected to increase. The abundance and diversity of different arthropod groups might, as a result of these environmental changes, be expected to change with increasing altitude, although responses are likely to vary among different taxa. For example, some groups or species may be widely distributed along an altitudinal gradient, while others might specialise in particular extremes of the climate continuum associated with changes in altitude. These distributions of individual organisms may be related to differences in life history, behaviour or interactions with other organisms associated with changes in environmental conditions (Hodkinson 2005) as is the case along other environmental gradients.

Given that temperature (Chen *et al.* 2009) and moisture are considered important influences

on arthropod life histories, arthropods, and in particular insects, would be expected to respond to environmental changes associated with changes in altitude. A simple correlation between known environmental conditions and the physiology, behaviour and life history of major arthropod groups might suggest *a priori* predictions of dominance of particular arthropod groups under different microclimatic conditions. For example, flies require moist conditions for larval development and this would suggest larger populations in moist environments. By contrast, for ants ground nesting is difficult under wet conditions and arboreal nesting is limited by cold conditions, so they would not be expected to be very successful in the cool wet conditions of mountain tops (Janzen 1973). Some general trends in pollinator dominance in relation to altitude have been identified in temperate systems. A decreasing number of plants are pollinated by Hymenoptera with increasing altitude, whereas Lepidoptera and in particular Diptera, become increasingly important pollinators along the same gradients (Arroyo *et al.* 1982; Warren *et al.* 1988). In these temperate systems, two explanations for these trends have been proposed. First, a reliance on endothermically generated energy in Hymenoptera, versus lengthy sun basking in the other two orders, may place them at a competitive disadvantage in higher, colder altitudes (Arroyo *et al.* 1982; Warren *et al.* 1988). In contrast, differences in flower morphology between high and low elevations was considered by Warren *et al.* (1988) to present a competitive advantage to Hymenoptera at lower elevations. This second hypothesis suggests that elevational patterns might be driven by competition among pollinators for flowers, rather than by competition between plant species for pollinators, as implied by the insect thermoregulatory basis of the former hypothesis. However, Warren *et al.* (1988) concluded that the dominance of flies at high altitudes (70% of the flora was pollinated by flies) was the result of insect physiology. By contrast, in reviewing the changing abundance of herbivorous insects with altitude, Hodkinson (2005) demonstrated that populations of individual species of flies, beetles and moths showed both increases and decreases with increasing altitude. His conclusion was that any a priori simple correlation with climatic change would be masked by complex interactions with other species of both plants and animals.

Lamington National Park in southeast Queensland, presents an opportunity to consider patterns of insect diversity along an altitudinal gradient. Lamington National Park supports extensive areas of subtropical rainforest (see Laidlaw *et al.* 2011 for a review of the rainforest types represented in the park) and encompasses altitudes ranging from approximately 250 m a.s.l. to close to 1200 m a.s.l. The IBISCA-Queensland Project (see Kitching *et al.* 2011) set out to determine the distribution of arthropod groups along an altitudinal gradient using multiple sampling methods. An altitudinal gradsect was established in Lamington National Park with four plots at each of five altitude categories (300, 500, 700, 900 and 1100 m a.s.l.) giving a total of 20 plots. Using these plots, a "baseline" arthropod survey was conducted in which a standard set of traps were deployed. Most of the baseline sampling methods were repeated in each of four seasons across a 12 month period. Details of the trapping program are provided in Kitching *et al.* (2011). Here we focus on two trapping methods – Malaise traps and flight intercept traps (FITs). Both methods capture a high number and diversity of flying insects, but Malaise traps are particularly effective at collecting Diptera and Hymenoptera (Campbell & Hanula 2007) while Coleoptera are particularly well sampled by flight intercept traps (Southwood & Henderson 2000).

Using the abundances of seven major arthropod groups collected over four seasons in both Malaise and flight intercept traps (FITs) we initially tested whether the overall abundance of different arthropod groups changed between seasons. We expected considerable differences in overall abundances between samples collected in the cool, dry winter (July) and those collected in other seasons. However, differences between

samples collected during the transition from the dry season to the wet season (October), the mid-wet season (January) and the end of the wet season (March) are less predictable. Our second aim was to determine if the overall abundance of different arthropod groups changed with increasing altitude. In particular, are there changes in the dominant arthropod groups from low to high altitudes? For example, we might expect an increase in Diptera and corresponding decrease in Hymenoptera at progressively higher altitudes. We then tested whether altitudinal patterns were consistent across all four sampled seasons. We also discuss the similarities and differences between the results of the two different trapping methods.

MATERIAL AND METHODS

Study site. Sampling was conducted at each of four IBISCA-Queensland plots established within five altitudinal zones (300, 500, 700, 900 and 1100 m a.s.l.) along an altitudinal gradsect in Lamington National Park as described in detail by Kitching *et al.* (2011). All plots were located on basalt derived soils with rainforest the broad vegetation type (Laidlaw *et al.* 2011). The area is characterised by summer dominant rainfall, with summer falls (on average 200 mm) reaching a peak in January. A comprehensive discussion of micrometeorological conditions of the plots can be found in Strong *et al.* (2011).

Trapping. Single Malaise and flight intercept traps (FITs) were placed within fifty metres of the post located in the centre of the 20 x 20 m quadrat of each of the twenty IBISCA-Queensland plots (see Kitching *et al.* 2011). In this way four trap replicates were obtained at each of five altitudes. The Malaise trapping program was described in detail in Lambkin *et al.* (2011). Each FIT consisted of a vertical rectangular panel (66 x 70 cm) of layers of transparent plastic kitchen film, wrapped around two wooden posts, above a rectangular collecting container (14 x 66 cm) raised above ground level and filled with propylene glycol. A roof was erected over the trap array to prevent water inundating the collection containers. Traps were operated for 10 days at each plot. Both Malaise and FIT traps were set and operated four times over the course of a twelve month period; October 2006, January 2007, March 2007 and July 2007. Samples were stored in 70% ethanol and returned to the laboratory for sorting. Individuals from all major arthropod groups were sorted and counted. Arthropod groups selected for analyses were Thysanoptera, Heteroptera, Diptera, Coleoptera, Hymenoptera and Araneae. In addition, Hymenoptera were subdivided into ants (family Formicidae) and all other Hymenoptera as this was easily achieved and we strongly suspected ants would respond to altitude. These groups are megadiverse arthropod taxa and those for which taxonomic expertise was available for further identification as part of the broader IBISCA-Queensland program. This paper reports only these seven taxa selected for further study.

Analysis. To determine if assemblages of the seven major arthropod taxa changed with altitude and if these trends were consistent among seasons, we used non-parametric multivariate two-way analysis of variance (NPMANOVA, Anderson 2001) using PRIMER 6 and PERMANOVA+ software packages (Clarke & Gorley 2006; Anderson *et al.* 2009). This approach makes no assumptions about underlying data distributions and generates a pseudo *F*-value analogous to the familiar parametric *F* of Fisher with probability values calculated by permutation (Anderson 2001). Separate analyses were conducted for Malaise and FIT samples, based on Bray-Curtis dissimilarity index values, using abundance data (log-transformed and then standardised by sample size), with 4999 permutations. Although this is a multivariate analysis analogous to repeated measures ANOVA, no correlation structures through time (sphericity) were assumed as sampling events were separated by an adequate amount of time (at least three months) (Anderson *et al.* 2009).

NPMANOVA was also used to make post-hoc pair-wise comparisons. Due to the small number of replicated samples per treatment, the number of unique permutations was limited for each pair-wise comparison. Consequently, Monte Carlo asymptotic permutation was conducted to calculate *P* values. Because of the number of pair-wise comparisons the chances of a Type I error increased and this should be taken into account when determining the significance of probability values (for example by applying a Bonferroni correction). Significant levels were, however, not changed as the minimum *P* value for 4999 permutations (P=0.002) was greater than Bonferroni corrected *P* values (e.g. P=0.001 for 40 pair-wise comparisons).

Non-metric multi-dimensional scaling (NMDS) was then used to create ordination plots for both the Malaise and FIT datasets to visually explore the results of the NPMANOVA. These ordinations were calculated using the software package PRIMER 6 (Clarke 1993; Clarke & Gorely 2006) using 25 restarts.

TABLE 1. Results of non-parametric multivariate analyses of variance carried out on the abundance of seven arthropod groups along an altitudinal gradient at four times of the year (seasons) using two insect trapping methods , Malaise traps and flight intercept traps (FITs).

		df	F	*P* (perm)
Malaise Traps	Season	3	32.4265	0.0002
	Altitude	4	3.8535	0.0002
	Season × Altitude	12	1.89791	0.0126
FITs	Season	3	34.3645	0.0002
	Altitude	4	6.7559	0.0002
	Season × Altitude	12	1.7985	0.0472

TABLE 2. Summary results of post-hoc tests comparing differences in ordinal assemblages between pairs of seasons using Malaise traps and FITs. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the five altitudinal zones. *P* values were calculated by 4999 Monte Carlo asymptotic permutations. Significant *P* values are shown in bold.

		P (MC) values				
Trap Method	Groups	300 m	500 m	700 m	900 m	1100 m
Malaise	Oct, Jan	0.084	0.256	0.123	0.091	0.103
	Oct, Mar	0.185	0.585	0.568	**0.009**	0.264
	Oct, Jul	**0.035**	**0.008**	**0.016**	**0.015**	**0.003**
	Jan, Mar	0.708	0.369	0.356	**0.046**	0.106
	Jan, Jul	**0.019**	**0.008**	**0.008**	0.081	**0.002**
	Mar, Jul	**0.044**	**0.007**	**0.027**	**0.035**	**0.003**
FITs	Oct, Jan	0.437	0.105	0.096	0.131	**0.029**
	Oct, Mar	0.160	0.086	**0.019**	**0.018**	**0.004**
	Oct, Jul	**0.006**	**0.005**	**0.008**	**0.008**	**0.006**
	Jan, Mar	0.239	0.821	**0.043**	**0.055**	**0.001**
	Jan, Jul	**0.002**	**0.019**	**0.006**	**0.006**	**0.002**
	Mar, Jul	**0.005**	0.088	**0.022**	**0.015**	**0.002**

TABLE 3. Summary results of post-hoc tests comparing differences in ordinal assemblages between pairs of altitudes collected in Malaise traps and FITs. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the four seasons. *P* values were calculated by 4999 Monte Carlo (MC) asymptotic permutations. Significant *P* values are shown in bold.

Trap Method	Groups	*P* (MC) values			
		October (spring)	January (summer)	March (autumn)	July (winter)
Malaise	300m, 500m	0.550	**0.015**	0.375	0.197
	300m, 700m	0.702	0.068	0.401	0.400
	300m, 900m	0.260	**0.011**	**0.044**	0.767
	300m, 1100m	0.425	**0.001**	0.126	**0.046**
	500m, 700m	0.753	0.148	0.776	0.189
	500m, 900m	0.623	0.068	**0.037**	0.135
	500m, 1100m	0.201	**0.008**	0.234	**0.030**
	700m, 900m	0.377	0.122	0.282	0.712
	700m, 1100m	0.163	**0.026**	0.186	**0.006**
	900m, 1100m	0.861	0.139	0.061	**0.019**
FITs	300m, 500m	0.484	0.644	0.752	0.309
	300m, 700m	0.180	0.396	0.174	0.141
	300m, 900m	0.307	0.114	0.077	**0.049**
	300m, 1100m	0.063	**0.005**	**0.047**	**0.009**
	500m, 700m	0.123	0.277	0.336	0.807
	500m, 900m	0.575	0.356	0.247	0.760
	500m, 1100m	0.107	**0.006**	0.334	0.245
	700m, 900m	0.269	0.162	0.506	0.303
	700m, 1100m	**0.043**	**0.002**	0.079	0.127
	900m, 1100m	0.183	**0.007**	0.439	0.570

RESULTS

The total number of individuals collected in each sample was highly variable. Malaise traps collected many more individuals (n = 187504) than did the FITs (n = 33487). There was, as expected, considerable seasonal variability with substantially less insects collected in the dry, cooler season (July 2007) compared to all other seasons. This was the case for both Malaise traps (July total = 25754) and FITs (July total = 4060). Total trap catches in July were less than half those in March (Malaise = 63385 and FITs = 8302) and January (Malaise = 63313 and FITs = 10887). In the case of the FITs, the October catch (12480) was almost three times the July catch. However, although higher than the July catch, the Malaise catch for October (37808) did not display the same large increase seen in the FITs. Diptera dominated (85% of the catch) the Malaise trap catches in all seasons and at all altitudes. While Diptera were a strong faunal element in the FIT catches (30%),

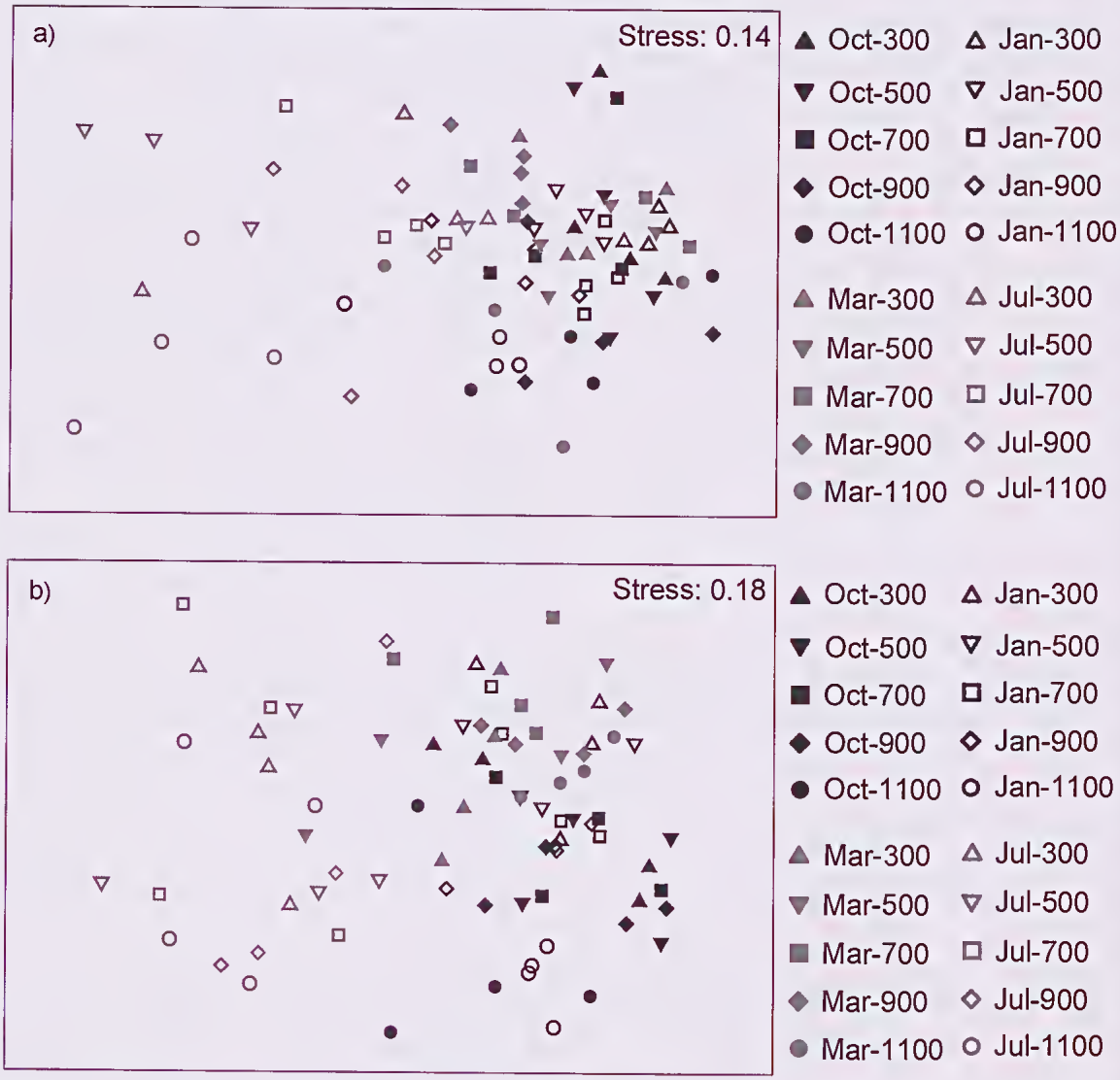


FIG. 1. Ordination plot based on a multi-dimensional scaling analysis of the relative abundance of seven arthropod taxa caught across five altitudinal zones (four plots in each of 300, 500, 700, 900 and 1000 m a.s.l.) in each of four seasons using (a) Malaise traps and (b) flight intercept traps.

Coleoptera were the most abundant group (54%) in these traps at all altitudes and in all seasons with the exception of July when Diptera were more abundant at all altitudes.

Altitude and Season. We first investigated the effects of altitude and season on the assemblage composition of the target arthropod groups. Although the results of NPMANOVA showed

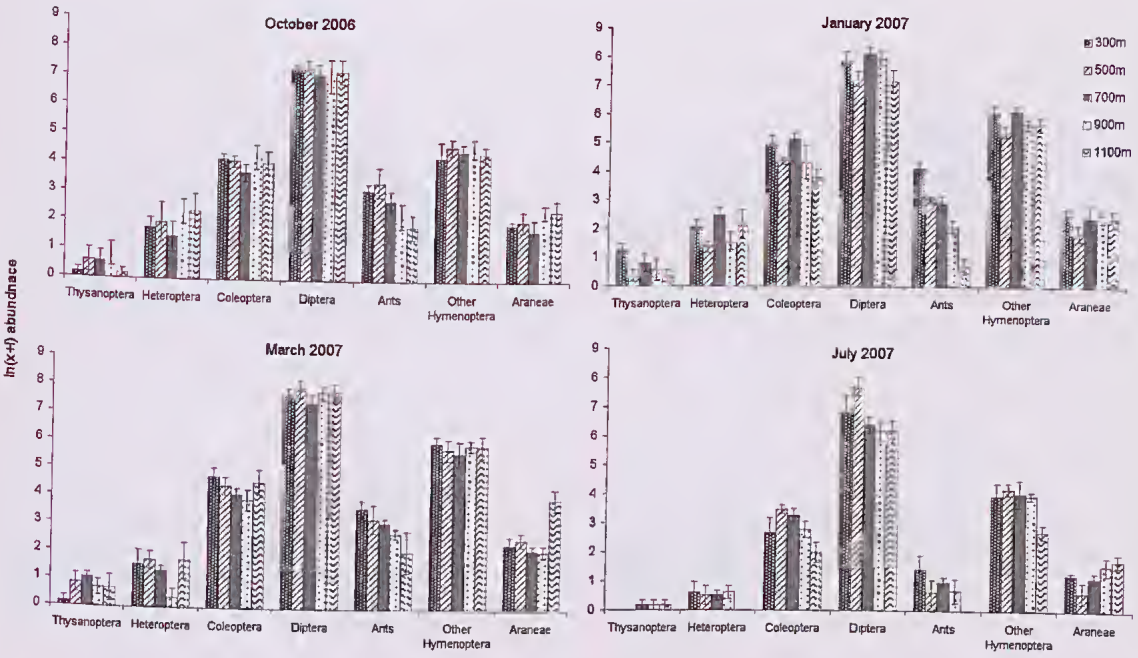


FIG. 2. Natural log-transformed (x+1) mean abundance (± S.E.) of arthropod groups caught by Malaise traps at four plots within each of five different altitudes (m a.s.l.) in four seasons; spring (October 2006), summer (January 2007), autumn (March 2007) and winter (July 2007).

significant effects of both season and altitude, their interaction effect was also significant for both trap methods (Table 1). This suggests that the differences between altitudes were expressed differently between seasons (and vice versa). Consequently post-hoc analyses were restricted to the investigation of arthropod assemblages between seasons within each of the five altitudes (Table 2), and investigation of arthropod assemblages between altitudes within each of the four seasons (Table 3).

The NPMANOVA procedure provides the capacity to test *a posteriori* pair-wise combinations of the interaction terms and when this was done for the interaction of season and altitude on the seven arthropod groups collected by Malaise traps, a number of pair-wise comparisons demonstrated a significant difference at $P < 0.05$ (Tables 2 and 3).

Looking first at changes in assemblages between seasons at individual altitudes, significant differences between at least two seasonal assemblages were experienced at all altitudes, with assemblages collected by FITs from 1100 m a.s.l. significantly different between all seasons (Table 2). Most frequently, winter samples (July) were significantly different to those from all other seasons (Table 2). When we consider changes in assemblages across altitude within each individual season, fewer significant pair-wise comparisons are apparent (Table 3). Most altitudinal change in assemblages was confined to winter (July) and summer (January) (Table 3), with only one significant difference (700 m v 1100 m FIT) demonstrated in spring (October). The assemblages of highest and lowest altitudes were more likely to be significantly different compared to those from adjacent altitudes (Table 3).

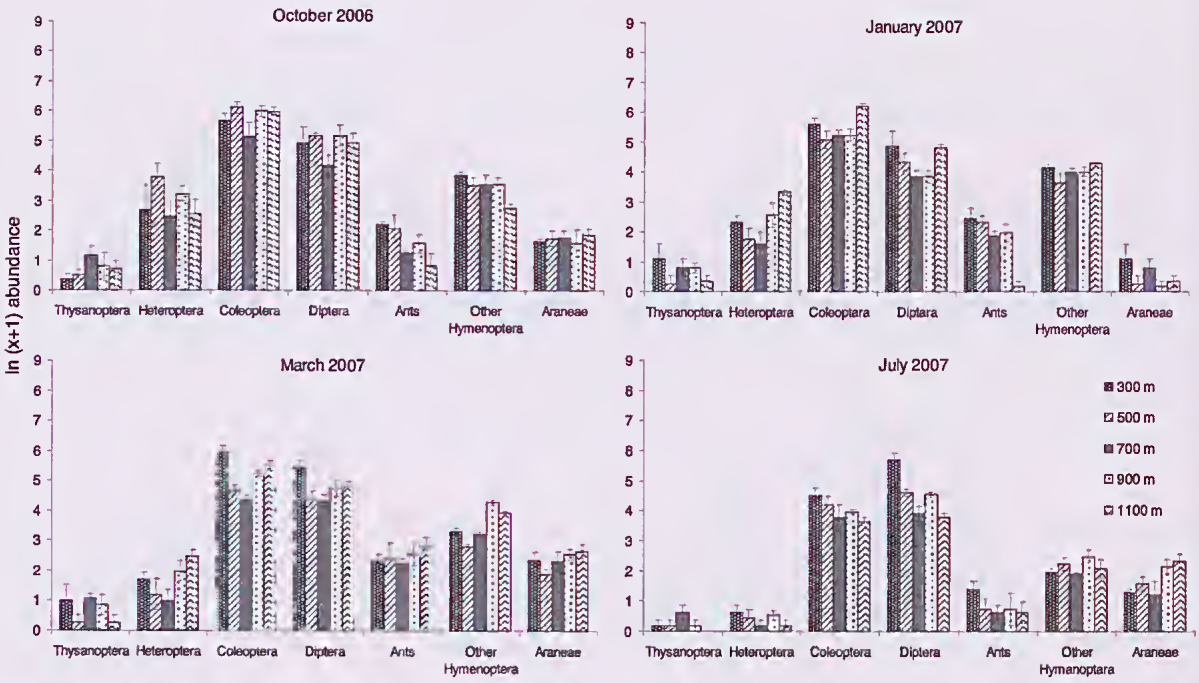


FIG. 3. Natural log-transformed (x+1) mean abundance (± S.E.) of arthropod groups caught by flight intercept traps at four plots within each of five different altitudes (m a.s.l.) in four seasons; spring (October 2006), summer (January 2007), autumn (March 2007) and winter (July 2007).

The complicated nature of the interaction of season and altitude on assemblages of the target taxa is apparent from the NMDS ordinations. The influence of season is somewhat easier to visualise, with winter samples (from both collecting methods) clearly separated from those of other seasons, but there is no clear altitudinal pattern of assemblages (Fig. 1).

When looking at the abundance data for individual taxa, there was no consistent altitudinal trend for all groups in all seasons (Figs 2 and 3). The abundances of some taxa appeared relatively constant across all altitudes, while for other taxa there did not appear to be a simple linear relationship between abundance and altitude. The Diptera are a case in point, with most seasons showing no clear pattern between abundance and altitude except for the July FITs samples where there was a steep decline in dipteran abundance with increasing altitude (Fig. 3). Ants showed the clearest altitudinal response, a linear-decline in abundance with increasing altitude, and this trend was consistent across most seasons and both trapping methods. Spiders either showed similar abundances across all altitudes or increased in abundance with increased altitude, with the clearest trend observed in July (Fig. 3).

DISCUSSION

Our results demonstrate that the abundance and community dominance of major arthropod taxa in response to increasing altitude is complex. The expectation that some groups would decline steadily with altitude, while others increased, was simply not the case (with the exception of ants). The total abundance of individuals did change from season to season, as was expected, with the

Malaise traps in particular collecting dramatically greater numbers of the focal taxa in the wet season months of January and March, indicating that most flight activity occurs during this time. The very low abundances recorded from both trapping methods in the drier and cooler winter season (July sample) is consistent with other seasonal surveys of tropical insect abundance (e.g. Frith & Frith 1985; Wilson *et al.* 2007).

The abundances of some of the focal arthropod groups changed consistently with respect to altitude, however, the patterns were not consistent across all seasons. In this study, season appeared to have the strongest influence on the abundances of the focal groups rather than altitude. However, this does not mean that altitude is unlikely to influence the abundance and dominance of some groups, but rather that the relationship between abundance and altitude is under a strong seasonal influence.

Strong seasonal differences were detected within altitudes, particularly between winter (July) samples and those of all other seasons. This was particularly the case for all altitudes and both trapping methods when assemblages from October and July were compared. Winter samples (July) were generally characterised by low total abundances at all altitudes, with substantially lower catches at 700 m a.s.l. and above. This contrasted to the situation in the wetter, warmer months (October, January and March) in which the total trap catches were lowest at either the 500 or 700 m a.s.l. plots. This pattern was apparent for all the mega-abundant groups, *viz.* Diptera, Coleoptera and Hymenoptera (excluding ants).

Significant differences in the assemblage composition of the focal taxa between different altitudes were detected, although almost exclusively in summer (January) and winter (July). This again emphasises the importance of season in determining the assemblage of arthropod groups at a given altitude. Hodkinson (2005), in a review of a number of altitudinal population studies of insects, concluded that there was no consistent response in abundance within Orders with both altitudinal increasers and decreasers found. Our study considers arthropods at a very coarse taxonomic scale, and the weak altitudinal patterns we observed are likely a reflection of the unique and inconsistent responses of the individual species within each order to altitude and therefore micro-climatic conditions. Our study does, however, emphasise the role of season in accentuating altitudinal responses. We know that insects at the extremes of their altitudinal range can have very different morphologies, behaviours and life history patterns (Hodkinson 2005). As the seasons and their climatic conditions shift, so too might the populations of species at the extremes of their ranges. Seasonal shifts in species have demonstrated the link between microclimatic conditions and shifting species distributions (Menéndez & Gutiérrez 2004).

In our study, abundances of Hymenoptera (excluding ants) did not display a consistent altitudinal trend, with just the October FIT and July Malaise samples showing an apparent decrease in abundance with increasing altitude. This contrasts with consistent declines in the importance of hymenopteran pollinators with increasing altitude found in temperate regions. Consequently we found no evidence of an endothermic disadvantage to Hymenoptera at cool, high altitudes (Arroyo *et al.* 1982; Warren *et al.* 1988).

CONCLUSIONS

The general intent of this study was to determine if the abundances and composition of major arthropod groups change with altitude and if such changes are consistent across seasons. The significant results of testing season, altitude and the interaction of these factors using the non-parametric MANOVA demonstrate that differences between altitudes in each season were not random. However it is difficult to determine a clear and consistent trend. The sampling effort at each altitude was restricted to four samples. The

highly variable catches in each trap suggest that greater numbers of replicates might give a clearer picture, although sorting more samples would be problematic. It is also important to bear in mind that this study looked only at one 12 month period. No doubt repeated ongoing surveys would help clarify patterns.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. The IBISCA-Qld Project would not have happened without the considerable efforts of Professor Roger Kitching. Prof. Kitching has also generously provided comments and feedback on the analysis used in this paper. Dr Geoff Monteith (Queensland Museum) ran the FIT traps throughout the IBISCA project and we thank him for allowing us to use the by-catch for this analysis. We would like to give particular thanks to the efforts of Dr Petrus Heyligers, Mr John Holt, Ms Sarah Maunsell and Mr Darren Bito for assistance with insect sorting. Drs Chris Burwell and Akihiro Nakamura provided significant comments on the original manuscript that greatly improved the final paper. S.L.B was the grateful recipient of an APA scholarship and Smart State top-up scholarship during the preparation of this manuscript. C.L.L. and N.T.S. were supported by funding from the Queensland Museum.

LITERATURE CITED

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.

Anderson, M.J., Gorley, R.N. & Clarke, K.R. 2009. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. (PRIMER-E: Plymouth).

Arroyo, M.T., Primack, R. & Armesto, J.J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany* 69: 82-97.

Campbell, J.W. & Hanula, J.L. 2007. Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation* 11: 399-408.

Chen, I.C., Shiu, H.J., Benedick, S., Holloway, J.D., Cheye, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* 106: 1479-1483.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143.

Clarke, K.R. & Gorley, R.N. 2006. *PRIMER v6: User Manual/Tutorial.* (PRIMER-E: Plymouth).

Frith, C.B. & Frith, D.W. 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* 10: 237-248.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80: 489-513.

Janzen, D.H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54: 687-708.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* 55(2): 235-230.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J., Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* 55(2): 271-290.

Lambkin, C.L., Boulter, S.L., Starick, N.T., Cantrell, B.K., Bickel, D.J., Wright, S.G., Power, N., Schutze, M.K., Turco, F., Nakamura, A. & Burwell, C.J. 2011. Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an

Australian subtropical rainforest: one hundred throusand and counting. *Memoirs of the Queensland Museum-Nature* **55**(2): 315-331.

Menéndez, R. & Gutiérrez, D. 2004. Shifts in habitat associations of dung beetles in northern Spain: climate change implications. *Ecoscience* **11**: 329-337.

Southwood, T.R.E. & Henderson, P.A. 2000. *Ecological Methods*. (Blackwell Science Ltd: Oxford).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Warren, S.D., Harper, K.T. & Booth, G.M. 1988. Elevational distribution of insect pollinators. *American Midland Naturalist* **120**: 325-330.

Wilson, R.D., Trueman, J.W.H., Williams, S.E. & Yeates, D.K. 2007. Altitudinally restricted communities of schizophoran flies in Queensland's Wet Tropics: vulnerability to climate change. *Biodiversity and Conservation* **16**: 3163-3177.

Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an Australian subtropical rainforest: one hundred thousand and counting!

Christine L. LAMBKIN[1]

Sarah L. BOULTER[2]

Noel T. STARICK[1]

Bryan K. CANTRELL[1]

Dan J. BICKEL[3]

Susan G. WRIGHT[1]

Narelle POWER[1]

Mark K. SCHUTZE[1, 4]

Federica TURCO[1]

Akihiro NAKAMURA[1,2]

Chris J. BURWELL[1,2]

1. Biodiversity Program, Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia. Email: christine.lambkin@qm.qld.gov.au; 2. Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia; 3. Department of Entomology, Australian Museum, 6 College Street, Sydney 2010 New South Wales; 4. Discipline of Biogeosciences & CRC National Plant Biosecurity, Queensland University of Technology, Brisbane Qld 4001, Australia.

Citation: Lambkin, C.L., Boulter, S.L., Starick, N.T., Cantrell, B.K., Bickel, D.J., Wright, S.G., Power, N., Schutze, M.K., Turco, F., Nakamura, A. & Burwell, C.J. 2011 12 20: Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an Australian subtropical rainforest: one hundred thousand and counting! *Memoirs of the Queensland Museum — Nature* 55(2) 315-331. Brisbane. ISSN 0079-8835.

ABSTRACT

Many surveys around the world have examined the altitudinal or seasonal variation of invertebrate biodiversity but few have concentrated on the fly fauna because of difficulties with the amount of material and identification. We examined family-level assemblages of flies collected in Malaise traps from rainforest at Lamington National Park, south-east Queensland across altitude and seasons. We found significant effects of both season and altitude on the overall abundance of other Diptera (without lower Diptera), with a significant interaction effect so that abundances in summer were much higher than those in winter, but only at mid to high altitudes. We also found significant effects of both season and altitude on the family richness of other Diptera, and again the interaction of these factors was significant. A clear seasonal influence was noted at mid to high elevations with a progressive decline in the number of fly families captured from summer to Spring to winter together with a decline with increasing altitude, at least in Spring and winter. Within each altitude, all seasonal fly assemblages were significantly different, with the exception of those from summer and autumn at 500 m a.s.l. However, the altitudinal responses of fly assemblages were less strong and not consistent between seasons. Six families were most strongly correlated with these patterns; Asilidae,

Chloropidae, Dolichopodidae, Empididae, Muscidae and Phoridae. Asilidae, Dolichopodidae and Empididae declined in abundance with increasing altitude. Only Chloropidae and Muscidae appeared to increase in abundance with altitude, at least between 700 and 1100 m but only in summer. Dolichopodids and muscids progressively declined in abundance as the sampling period became cooler, while asilids were captured throughout the transect in summer, were collected from only the two lowest elevations in Spring, and were completely absent in winter. All families had a limited presence at higher altitudes during July, the coldest and driest month. The Empididae, Phoridae, Chloropidae, and Drosophilidae appear to be able to survive at lower altitudes in winter, and become more abundant at higher cooler altitudes in summer. Generalist behaviours, lack of host specificity, larvae within the protected soil or leaf litter habitat, and ability as adults to fly considerable distances may provide many fly families with the capacity to cope with climate change, as they have in the past. ❐ *Diptera, altitude, seasonality, IBISCA-Queensland, Malaise traps.*

Studies of altitudinal gradients offer an ideal opportunity to study natural variability of plant and animal populations across a range of climatic conditions. Consequently, these studies may offer a tool for predicting responses of these organisms to changes in climate. Invertebrates represent a huge proportion of rainforest biodiversity and are considered vital for ecosystem function. The distribution of many invertebrate groups along altitudinal gradients, however, is poorly known, largely because of the massive diversity of invertebrates (see review in Novotny & Basset 2000) and most altitudinal studies have focussed on a subset of animals. Commonly studied groups include beetles (Coleoptera) (Erwin 1982; Escobar *et al.* 2005; Monteith & Davies 1991), moths and butterflies (Lepidoptera) (Brehm *et al.* 2007; Brehm & Fiedler 2003; Fleishman *et al.* 2000; Wilson *et al.* 2007b), ants (Hymenoptera, Formicidae) (Botes *et al.* 2006; Bruhl *et al.* 1999; Fisher 1996, 1999; Sanders *et al.* 2007), and spiders (Araneae) (Chatzaki *et al.* 2005; Monteith & Davies 1991). Few studies have considered the turnover of fly (Diptera) species along an altitudinal gradient (McKie *et al.* 2005; Wilson *et al.* 2007a; Yeates 1985). Yet the Diptera offer a potentially useful study group in ecological surveys encompassing a wide range of anatomical and biological specialisations (Yeates *et al.* 2009) and probably the widest range of ecological roles of the four mega-diverse insect orders (Kitching *et al.* 2004, 2005). In addition they can be systematically sampled with ease and represent a manageable number of families for identification (159 families, Yeates *et al.* 2009) making them a useful group to understand not only species turnover with altitude and therefore climate shifts, but also changes in ecosystem function along these natural gradients.

Direct altitudinal impacts on insects include changes to wing morphology associated with reduced flight activity, colour polymorphism to adjust body temperature at different altitudes, and variations in body size, phenology and fecundity (Hodkinson 2005). Additionally, changes in insect abundance and community composition might be expected in response to changes in environmental conditions associated with increasing altitude. However clear linear relationships are rarely found, for example, increases and decreases in species richness with increasing altitude, as well as mid-altitude peaks, have been reported previously (see review in Hodkinson 2005). Evidence of species turnover of flies with increasing altitude has been found in a number of studies (McKie *et al.* 2005; Wilson *et al.* 2007a; Yeates 1985). A survey of aquatic midges (Chironomidae) along altitudinal and latitudinal gradients found cool-adapted Gondwanan chironomids were more abundant at higher altitudes (McKie *et al.* 2005). In the case of schizophoran flies in the Australian Wet Tropics, Wilson *et al.* (2007a) determined that some morphospecies were found only at the upper limits of the studied altitudinal gradients. Furthermore, an increased dominance of flies visiting flowers at higher altitudes was attributed to their ability to use lengthy sun

basking, rather than relying on endothermically generated energy, to provide a competitive advantage in higher, colder altitudes (Arroyo *et al.* 1982; Kearns 1992; Warren *et al.* 1988).

Fly abundance and diversity can also be expected to vary in relation to season. For example, a 15 month survey of stiletto flies (Therevidae) in the Brisbane region demonstrated biannual peaks in abundance in Spring and autumn (Power 1998). Wilson *et al.* (2007a) demonstrated that the season of peak abundance for schizophoran flies changed with altitude in the Wet Tropics of Australia.

The IBISCA-Queensland Project (Kitching *et al.* 2011) was designed to document the current distributions of a wide range of invertebrate taxa along an altitudinal gradient within continuous subtropical rainforest in Lamington National Park, southeast Queensland. The aim was to identify taxa or suites of taxa that could be incorporated into long-term monitoring programmes to detect the impacts of climate change. This was achieved by employing a variety of sampling methods to collect invertebrates from a wide range of microhabitats. The aims of this study were to examine the altitudinal change in fly assemblages and to determine if this varied seasonally within subtropical rainforest at Lamington National Park, southeast Queensland.

METHODS

Study site

Sampling was conducted along the IBISCA-Queensland transect established within continuous subtropical rainforest in Lamington National Park at latitude 28°S. The transect ranged from 250 to 1140 m above sea level (a.s.l.) with four plots established at each of five altitudinal categories; 300, 500, 700, 900 and 1100 m a.s.l., giving a total of 20 plots. A description of the project aims is provided in Kitching *et al.* (2011), and Laidlaw *et al.* (2011) provide a description of the associated vegetation.

Malaise trapping

To give a true indication of groups present at a site during a faunal survey, it is desirable to employ a collecting method that is unbiased and operates continually. The most effective means of obtaining specimens, and temporal and geographic distributional data, is the use of passive collecting methods (Darling & Packer 1988; Evans & Owen 1965). Malaise traps are a passive, unbiased, flight intercept sampling method that collects insects as they move through the air. The Malaise trap, first described by René Malaise (1937), is a bilateral trap; essentially an open-sided tent with entrances from both sides and an angled roof leading up to an apex where a collection chamber attaches to a removable collecting jar in which insects are killed and preserved (Southwood 1978). Townes (1972) found that a bicoloured trap (i.e. a combination of light flaps and a dark intercepting baffle) increased the catch by 70% (in shade) to 180% (in sunlight) compared to an all white trap. As Malaise traps may be left unattended for several days, they are useful for the study of insect fauna in areas that are difficult to access (Lambkin *et al.* 2002; Malaise 1937; Townes 1962, 1972) such as the dense rainforest in which this study was conducted. They sample fauna throughout the daily cycle and in all weather. The chief difficulty is finding a suitable location for the Malaise traps as they sample insects moving through a relatively small landscape. Where possible, we placed Malaise traps perpendicularly across observed flight paths, across gullies, or in sunlit clearings.

A single Malaise trap was operated for 10 days at each of the four plots located at each of the five altitudes (total of 20 traps) during October 2006 and January and July 2007. Half the Malaise traps used were a standard Townes design (Townes 1962, 1972) and obtained from Australian Entomological Supplies, New South Wales. The remaining traps were modified Townes traps with curved roof panels designed by Michael Sharkey and manufactured by Sante Traps, Kentucky. Although we used Malaise

traps of two slightly different designs we consider they had similar performance. All Malaise traps used were made of very fine mesh, were 2 m high at the head, with central panel about 2 m long, and had a white roof, and black walls and central barrier. The head, four corners, and tail of the roof were tied by ropes to vegetation and the base pegged to open the trap to its maximum width. The collecting jars were filled with at least 300 ml of 95% ethanol. Generally all four Malaise traps at a particular altitude were erected on the same day. In 2006 all traps were installed from 5-9 October and cleared from 15-19 October. In January 2007 traps were installed between the 13th and 16th and cleared between the 23rd and 26th. In July 2007 traps were installed between the 15th and 18th and cleared between the 25th and 28th.

Sorting

All Diptera were extracted from samples and sorted into lower Diptera (previously the Suborder Nematocera), lower Brachycera (previously Orthorrhapha and Cyclorrhapha Ashiza) and Schizophora. Specimens of lower Diptera within each sample were counted but not further identified. All specimens of lower Brachycera and Schizophora (collectively the Brachycera) in samples were sorted to family level and counted. Brachyceran families were identified using interactive Lucid 'On the Fly' keys (Hamilton *et al.* 2006) and a self-generated photographic guide to representatives of every brachyceran family found during the study (Figs 1-2).

Analyses

Lower Diptera were not sorted to family level but this group potentially comprised 23 families. Due to ubiquity and overwhelming abundance of lower Diptera along the transect, and its taxonomic inconsistency with the rest of the family-level data, we analysed the total abundance of this group separately and did not incorporate it within assemblage-level multivariate analyses.

We tested the influence of two main factors, season (Spring, summer and winter) and altitude (300, 500, 700, 900 and 1100 m a.s.l.), and their interaction, on various aspects of fly diversity using PERMANOVA (permutational multivariate analysis of variance) available from PRIMER 6 (Clarke & Gorley 2006) and PERMANOVA+ add-on software packages (Anderson *et al.* 2008). PERMANOVA executes multivariate ANOVA, using permutation methods, to calculate *P* values derived from pseudo-*F* statistics of the distance measures. Effects of altitude and season were incorporated in the analyses as fixed factors and separate analyses were conducted for univariate (e.g. total abundance) and multivariate (family assemblages) response variables. Although PERMANOVA is designed primarily for multivariate analysis, univariate analysis is possible using Euclidean distances which yield Fisher's traditional univariate *F* statistic (Anderson *et al.* 2008). Univariate response variables included the total abundance of lower Diptera, the total abundance of other Diptera (lower Brachycera and Schizophora) and the family richness of other Diptera (i.e. the number of families per sample). Total abundance data were natural log-transformed, ln(x+1), before analyses. Multivariate analyses were performed on Bray-Curtis distance measures between plots, based on the natural log-transformed abundances of fly families (lower Brachycera and Schizophora). Type III sums of squares were used to calculate pseudo-*F* statistics, and *P* values were obtained using 9999 permutations of residuals under a reduced model. Post-hoc pairwise tests were used to compare differences between pairs of individual treatments, using a multivariate version of the t-statistic and Monte Carlo asymptotic *P* values (which are not restricted by the number of unique permutations). We also used PRIMER 6 to generate non-metric multidimensional-scaling (NMDS) ordinations (Clarke 1993) based on Bray-Curtis similarity matrices of fly families calculated between each plot pair, with 100 random restarts.

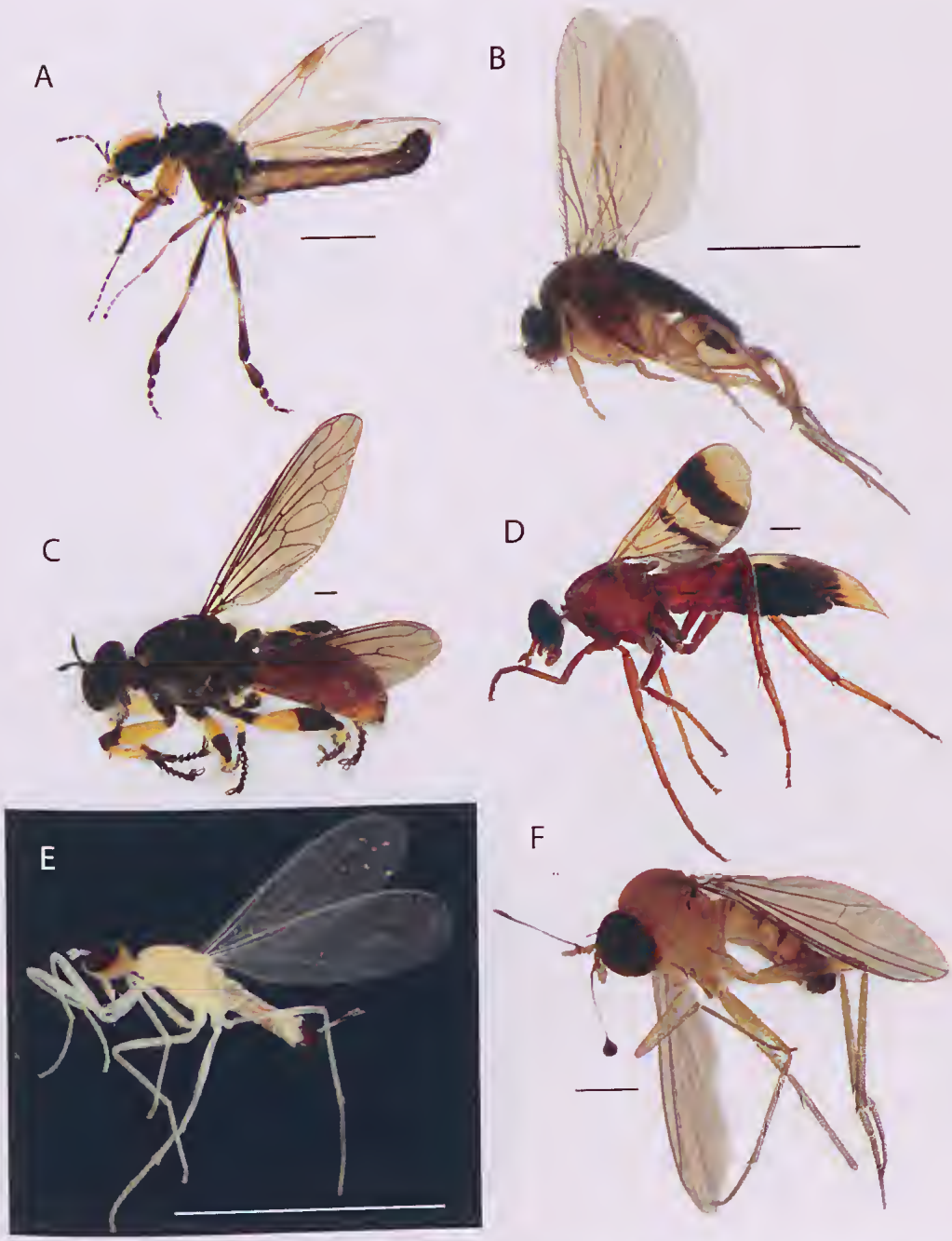


FIG. 1. Examples of fly families collected in IBISCA-Queensland in Malaise traps used in the easy visual guide for sorting prepared from photographs taken by N. Starick.A, *Dilophus* sp. Bibionidae, lower Diptera; B, Phoridae; C, *Laphria hirta* Ricardo, Asilidae; D, Undescribed genus and species of Therevidae; E, Hemerodromiinae, Empididae; F, *Yumbera callida* Parent, Dolichopodidae. Scale line = 1mm.

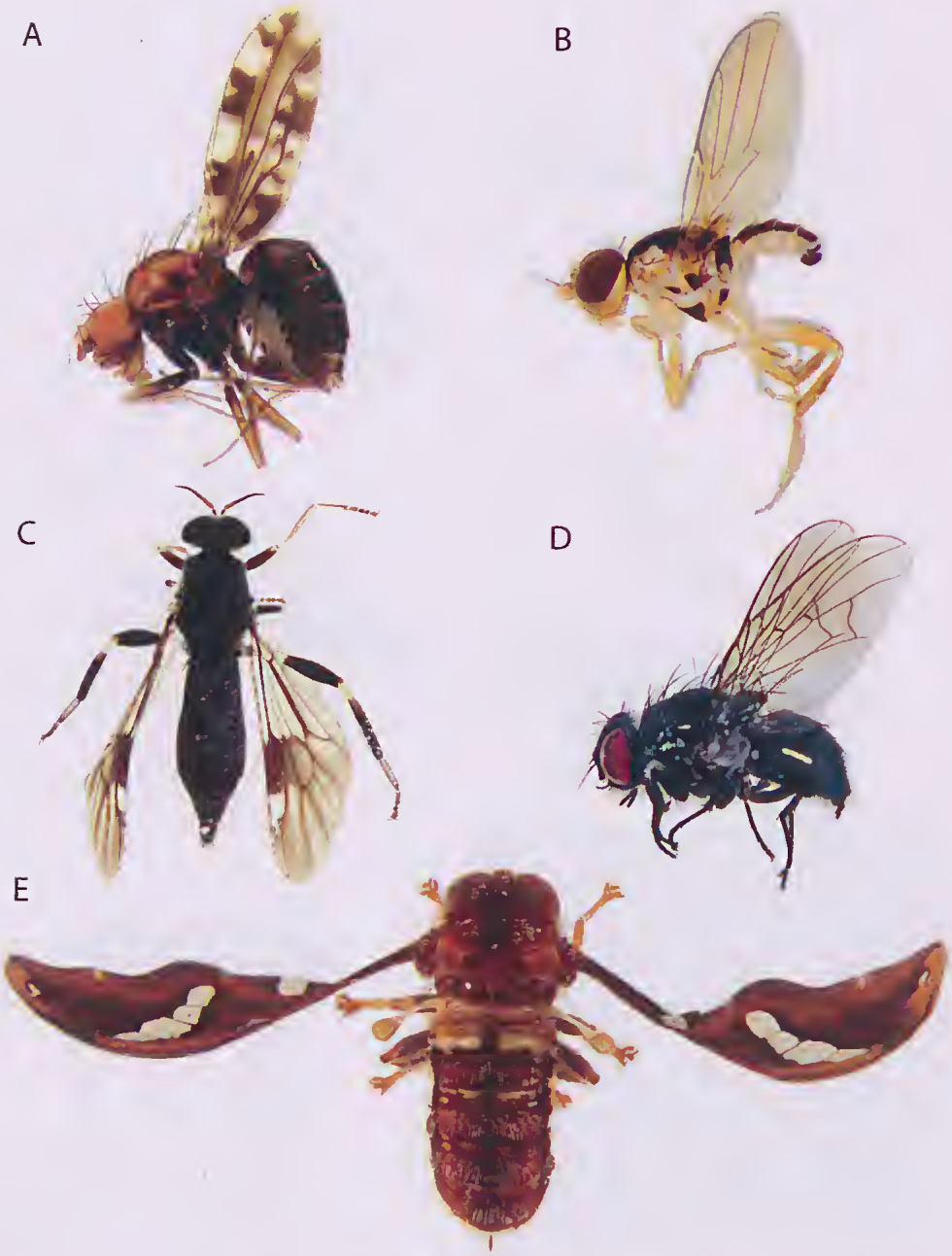


FIG. 2. Examples of fly families collected in IBISCA-Queensland in Malaise traps used in the easy visual guide for sorting prepared from photographs taken by N. Starick. A, *Tambourella endiandrae* Wheeler, Drosophilidae; B, Chloropidae; C, *Exaireta spinigera* (Wiedemann), Stratiomyidae; D, Muscidae; E, *Nycterimorpha speiseri* Lichtwardt, Nemestrinidae. Scale line = 1mm.

TABLE 1. Total numbers of individual Diptera in higher taxonomic groups and families collected at five altitudes (m above sea level) and during three seasons (October, January and July) using Malaise traps in Lamington National Park. Lower Diptera is 'Nematocera'.

Group	Family	300m	500m	700m	900m	1100m	Oct-06	Jan-07	Jul-07	Grand Total
Lower Diptera										
	Lower Diptera	17983	14954	19649	16532	13222	26173	41183	14984	82340
Orthorrhapha										
	Asilidae	53	12	18	6	4	14	79		93
	Bombyliidae	3		2				5		5
	Dolichopodidae	586	210	164	132	96	470	616	102	1188
	Empididae	545	329	241	280	84	629	730	120	1479
	Hybotidae	4		1	2		3	4		7
	Nemestrinidae		1					1		1
	Rhagionidae	8	14	6	5	8	35	6		41
	Stratiomyidae	184	61	87	51	7	168	211	11	390
	Tabanidae	2		1	5	1	1	8		9
	Therevidae	22	11	9	3		15	30		45
Cyclorrhapha Aschiza										
	Phoridae	4460	7036	3024	4050	1611	4704	7522	7955	20181
	Pipunculidae	18	10	6	1		12	22	1	35
	Platypezidae	8	7	10	15	2	5	37		42
	Sciadoceridae		1	1		2	2		2	4
	Syrphidae	31	2	6	3	3	6	39		45
Cylorrhapha Schizophora										
	Agromyzidae	4			1		1	2	2	5
	Anthomyidae	3					2		1	3
	Asteiidae	1						1		1
	Rhinophoridae		1		3			4		4
	Calliphoridae	8	4	7	67	120	14	192		206
	Chloropidae	177	333	138	172	149	281	465	223	969
	Clusiidae	12	13	9	13	17	19	30	15	64
	Cryptochaetidae	2						2		2
	Cypselosomatidae		2					2		2
	Drosophilidae	112	288	86	351	64	73	527	301	901
	Ephydridae	2	4	3		7	10	3	3	16
	Heleomyzidae	54	47	29	39	29	85	47	66	198

TABLE 1 continued...

Group	Family	300m	500m	700m	900m	1100m	Oct-06	Jan-07	Jul-07	Grand Total
	Helosciomyzidae		1	4	1	124	36	89	5	130
	Lauxaniidae	28	34	29	43	54	81	54	53	188
	Lonchaeidae	3	2		1		4		2	6
	Micropezidae	13	2	6	1		9	13		22
	Milichiidae	4	8	2	7	4	20	5		25
	Muscidae	153	51	108	119	255	209	436	41	686
	Neriidae	4	1				4	1		5
	Neurochaetidae		3					2	1	3
	Platystomatidae	5	4			2		11		11
	Pyrgotidae			2				2		2
	Sarcophagidae	8	1	2			1	9	1	11
	Sepsidae	7	7	2		4	9	6	5	20
	Sphaeroceridae	273	159	58	103	158	396	200	155	751
	Tachinidae	88	19	44	63	37	29	217	5	251
	Tanypezidae	6	1	1			5	3		7
	Tephritidae	2	3	3	3	4	3	10	2	15
	Teratomyzidae	1	22	8	6	4	2	9	30	41
Total no. individuals		24877	23658	23766	22078	16072	33530	52835	24086	110451
Number of families		38	37	34	30	27	36	42	25	45

Finally, a Bio-Env procedure (available from the BEST routine of PRIMER 6) was executed to find a subset of fly families that best 'explained' the overall pattern of whole (all families) fly assemblages. Bio-Env generates all possible combinations of the subset of fly families and compares their similarities to the whole fly assemblages using a selected rank correlation method (Clarke & Gorley 2006). We set the maximum number of fly families included in subsets to five and used Spearman rank correlation.

RESULTS

A total of 110451 fly specimens were collected across the three seasons and five altitudinal zones (Table 1). Lower Diptera dominated, comprising 74.5% of the total catch. The remaining flies (28111 specimens) were represented by 44 families, with most specimens from the family Phoridae (in the lower Brachycera); 20181 specimens representing 18.3% of the total fly specimens. Of the remaining 7930 specimens around 80% were comprised of seven families; Empididae (18.6%) (Fig. 1E), Dolichopodidae (14.9%) (Fig. 1F), Chloropidae (12.2%) (Fig. 2B), Drosophilidae (11.4%) (Fig. 2A), Sphaeroceridae (9.5%), Muscidae (8.7%) (Fig. 2D) and Stratiomyidae (4.9%) (Fig. 2C).

Fly abundance and family richness

The total abundance of flies (lower and other Diptera combined) declined considerably from summer to Spring to winter (52835 to 33530 to 24086 specimens respectively) and gradually

TABLE 2. Summary results of PERMANOVA tests, showing pseudo-*F* and *P* values of the two main factors, altitude and season, and their interaction. Four separate tests were conducted for three univariate response variables and fly assemblage data. Degrees of freedom for altitude, season, interaction and residual are 4, 2, 8 and 45 respectively. Lower Diptera is 'Nematocera' and other Diptera is 'lower Brachycera' + Schizophora.

	Altitude		Season		Interaction	
	Pseudo-*F*	*P*	Pseudo-*F*	*P*	Pseudo-*F*	*P*
Univariate analyses						
Abundance (lower Diptera)	0.535	0.713	9.431	**<0.001**	1.351	0.237
Abundance (other Diptera)	5.294	**0.001**	10.397	**<0.001**	5.695	**<0.001**
Family richness (other Diptera)	10.583	**<0.001**	70.992	**<0.001**	3.492	**0.002**
Multivariate						
Family assemblage (other Diptera)	4.594	**<0.001**	17.48	**<0.001**	3.081	**<0.001**

TABLE 3. Summary results of post-hoc tests comparing differences in fly family assemblages between pairs of seasons. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the five altitudinal zones. P values were calculated by 9999 Monte Carlo (MC) asymptotic permutations. Significant *P* values are shown in bold.

	P (MC) values				
Groups	300 m	500 m	700 m	900 m	1100 m
Oct, Jan	**0.044**	0.082	**0.033**	**0.040**	**0.014**
Oct, Jul	**0.009**	**0.008**	**0.007**	**0.035**	**0.014**
Jan, Jul	**0.007**	**0.008**	**0.002**	**0.004**	**0.003**

TABLE 4. Summary results of post-hoc tests comparing differences in fly family assemblages between pairs of altitudes. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the three seasons. *P* values were calculated by 9999 Monte Carlo (MC) asymptotic permutations. Significant *P* values are shown in bold.

	P (MC) values		
Groups	October (spring)	January (summer)	July (winter)
300m, 500m	**0.019**	0.122	**0.033**
300m, 700m	**0.012**	0.280	**0.038**
300m, 900m	**0.010**	0.058	**0.043**
300m, 1100m	**0.003**	**0.008**	**0.021**
500m, 700m	0.135	0.432	**0.006**
500m, 900m	0.241	0.212	**0.013**
500m, 1100m	**0.017**	**0.033**	**0.004**
700m, 900m	0.305	0.588	0.257
700m, 1100m	**0.013**	**0.020**	0.092
900m, 1100m	0.127	0.091	0.194

declined with increasing altitude (24 877 specimens at 300 m a.s.l. to 16 072 at 1100 m, see Table 1). The family richness of the other Diptera showed similar seasonal (41 families in summer, 36 in Spring and 24 in winter) and altitudinal (38 families at 300 a.s.l. declining to 26 at 1100 m a.s.l, see Table 1) patterns.

We found no significant effect of altitude on the abundance of lower Diptera (Table 2) which occurred in high numbers across all elevations (Fig. 3A). However, we did find a significant effect of season (Table 2), with post-hoc pair-wise comparisons showing significantly fewer lower Diptera collected in July (Fig. 3A). In contrast, we found significant effects of both season and altitude on the overall abundance of other Diptera, but we also found a significant

interaction effect (Table 2). There appeared to be a strong seasonal influence, with abundances in January much higher than those in July, but only at mid to high altitudes (700-1100 m) (Fig. 3B). It was difficult to discern any meaningful influence of altitude on the abundance of other Diptera as seasonal responses were highly idiosyncratic (Fig. 3B). Similarly, we found significant effects of both season and altitude on the family richness of other Diptera, and again the interaction of these factors was significant (Table 2). As with the abundance, there appeared to be a clear seasonal influence at mid to high elevations with a progressive decline in the number of fly families captured from January to October to July (Fig. 3C). There also appeared to be a trend for the number of fly families to decline with increasing altitude, at least in October and July (Fig. 3C).

Fly family-level assemblages

Initially we looked for patterns in family-level fly assemblages using NMDS ordination, incorporating samples from all seasons and altitudes (based on natural log-transformed abundances of fly families excluding lower Diptera). There appeared to be a seasonal pattern with samples collected in January (summer) and July (winter) clearly separated, whereas those from October (Spring) were intermediate (Fig. 4A). In contrast, the effect of altitude was much less apparent in the ordination (Fig. 4B).

Although we found significant effects of both season and altitude on family-level assemblages, we also found a significant interaction between these main factors (Table 2). Consequently post-hoc analyses involved investigation of fly assemblages between seasons within each of the five altitudes, and investigation of fly assemblages between altitudes within each of the three seasons.

Within each altitude, all seasonal fly assemblages were significantly different, with the exception of those from October and January at 500 m a.s.l. (Table 3). However, the altitudinal responses of fly assemblages were less strong and not consistent between seasons. In October, assemblages at the lowest (300 m) and highest (1100 m) altitudes were distinct, although there was no significant difference between those at 1100 and 900 m (Table 4). In January only assemblages from the highest elevation were significantly different, but again not from those at 900 m (Table 4). In stark contrast, July assemblages from the two lowest elevations (300 and 500 m) were significantly different from those at higher elevations, and from each other (Table 4). These results are supported by the NMDS ordinations which in October and January have the 300 and 1100 m assemblages widely separated with those of intermediate altitudes scattered between (Fig. 5A, B). The pattern in July was idiosyncratic with the samples from 300 and 500 m having distinct assemblages, whereas there were no apparent patterns among the other altitudes (Fig. 5C).

The Bio-Env procedure selected subsets of five fly families that were highly correlated with the pattern of fly assemblages based on all families. Only six families were included in the three most strongly correlated subsets (correlation coefficient 0.890-0.892); Asilidae, Chloropidae, Dolichopodidae, Empididae, Muscidae and Phoridae. Examining the individual abundances of these families across altitude in each sampling period, no consistent trend was apparent (Fig. 6). Three families (Asilidae, Dolichopodidae and Empididae) declined in abundance with increasing altitude (Fig. 6A, C, D). Only the Chloropidae (Fig. 6B) and Muscidae (Fig. 6E) appeared to increase in abundance with altitude, at least between 700 and 1100 m a.s.l., but only in the summer (January) sampling period. Some fly families showed clear seasonal signals. Dolichopodids and muscids progressively declined in abundance as the sampling period became cooler (Fig. 6C, E), while asilids were captured throughout the transect in summer, were collected from only the two lowest elevations in Spring, and were completely absent in winter (Fig. 6A). All families had a limited

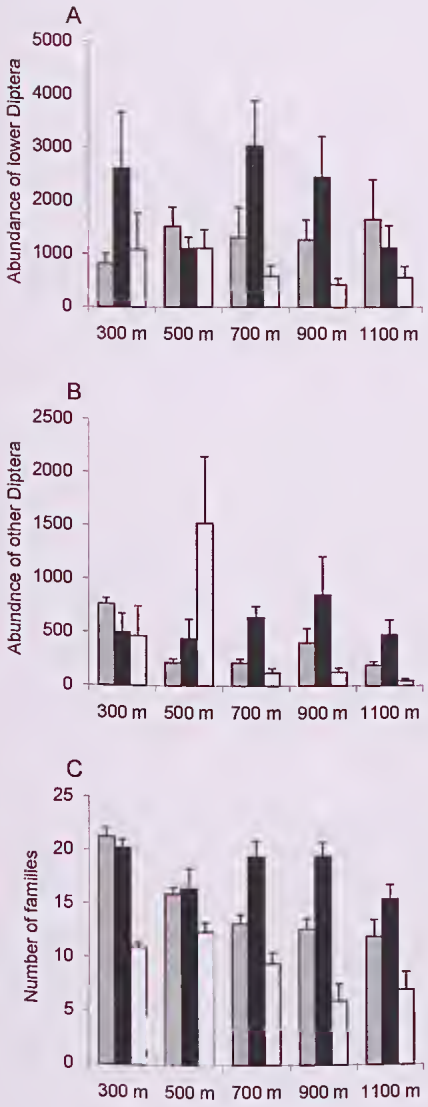


FIG. 3. Mean (+SE) values of A, total abundance of lower Diptera (= 'Nematocera'); B, total abundance of other Diptera (= 'lower Brachycera' and Schizophora), and; C, total number of fly families across five altitudes and three seasons, spring (October) shaded bars, summer (January) solid bars and winter (July) open bars.

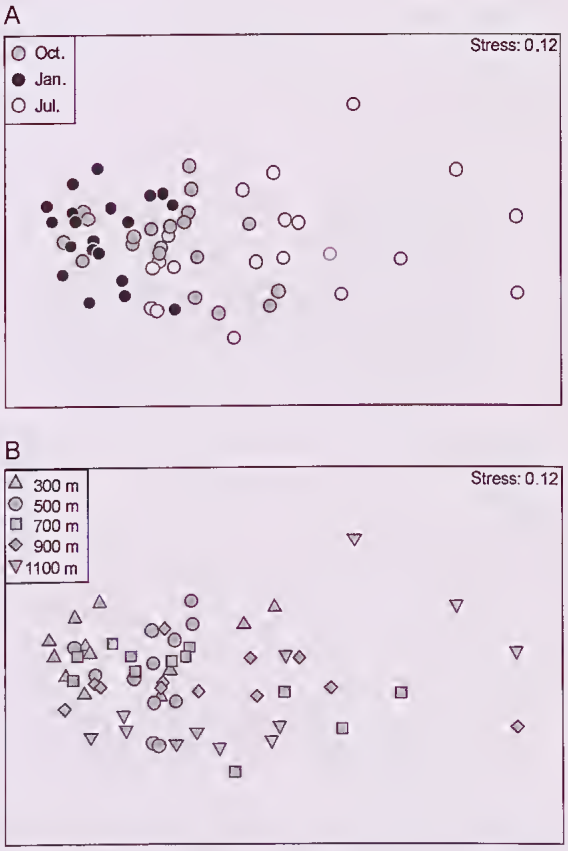


FIG. 4. NMDS ordinations of family-level fly assemblages based on log-transformed abundances (excluding lower Diptera). The same ordination was generated twice to visually present; A, seasonal and; B, altitudinal variations in assemblage composition.

presence at higher altitudes during July, the coldest and driest month.

DISCUSSION

The present study demonstrates the overwhelming presence of flies along the altitudinal gradient and across all sampling periods. It also demonstrates the complex response of different fly groups to environmental factors associated with both season and changes in altitude. A significant part of the fly fauna were those flies that made

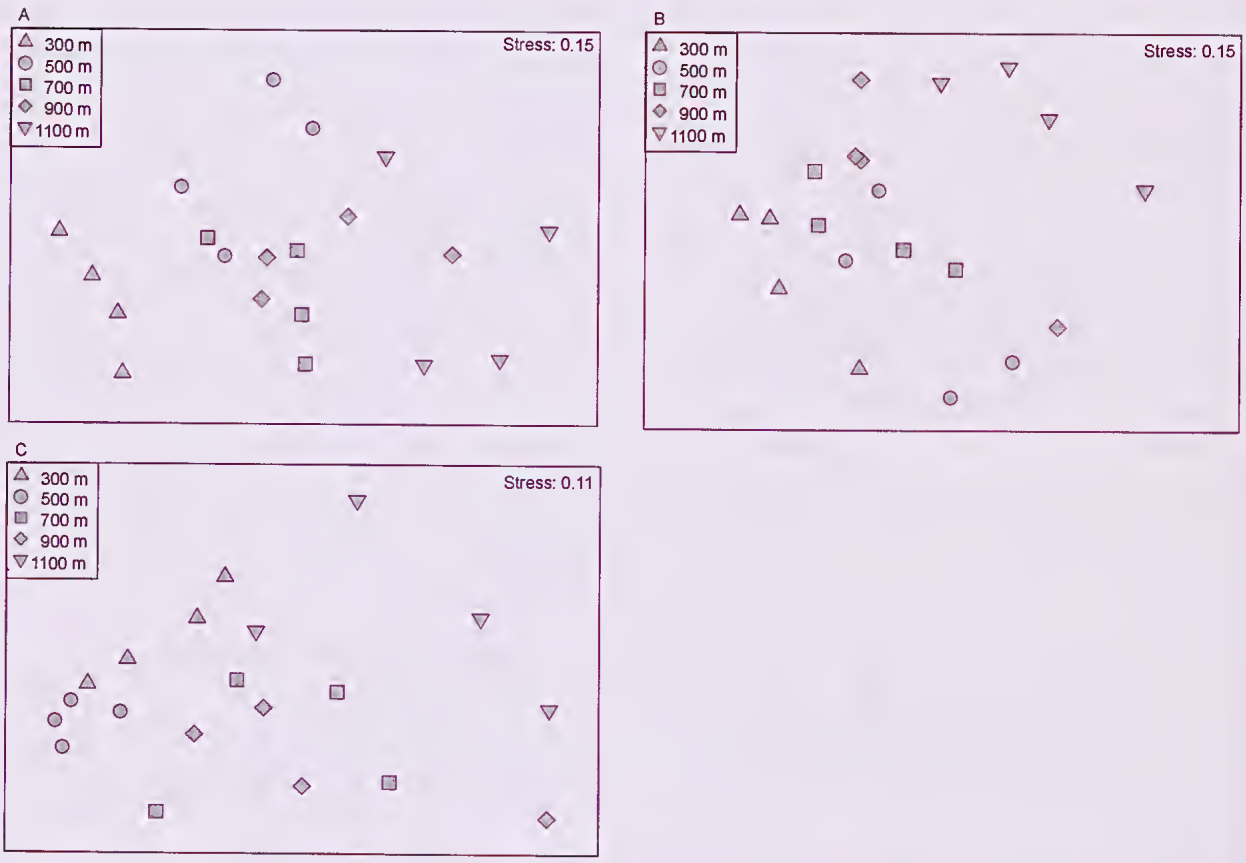


FIG. 5. NMDS ordinations of family-level fly assemblages based on log-transformed abundances (excluding lower Diptera). Three separate ordinations were generated for fly assemblages collected in A, October; B, January and; C, July.

up the lower Diptera. Although further sorting is required to determine an assemblage response to changes in altitude and season, it was clear that the lower Diptera are a conspicuous part of the insect fauna at all altitudes, whose numbers diminish in cooler, drier seasons.

The remaining flies, the lower Brachycera and Schizophora (other Diptera), did show changes in overall abundance and family richness, as well as different community assemblages among altitudes. Overwhelmingly, however, this response was modified by a strong seasonal influence, with altitudinal patterns differing between seasons. Identifying a clear, altitudinal "gradient" response is difficult and the lack of clear result is likely to reflect several factors: 1) the divergent environmental requirements of both immature and adult flies, with the unique responses of individual families contributing to the lack of pattern, 2) the coarse taxonomic level at which this analysis was undertaken (i.e. family) with individual species likely to have unique responses; and 3) the limited time period (10 days) over which samples were taken (e.g. trapping could coincide with a mass emergence of a particular family in a particular location). Nonetheless, some consistent responses are apparent. First, winter (July) sees a marked decrease in abundance and family richness across all altitudes. Second, the

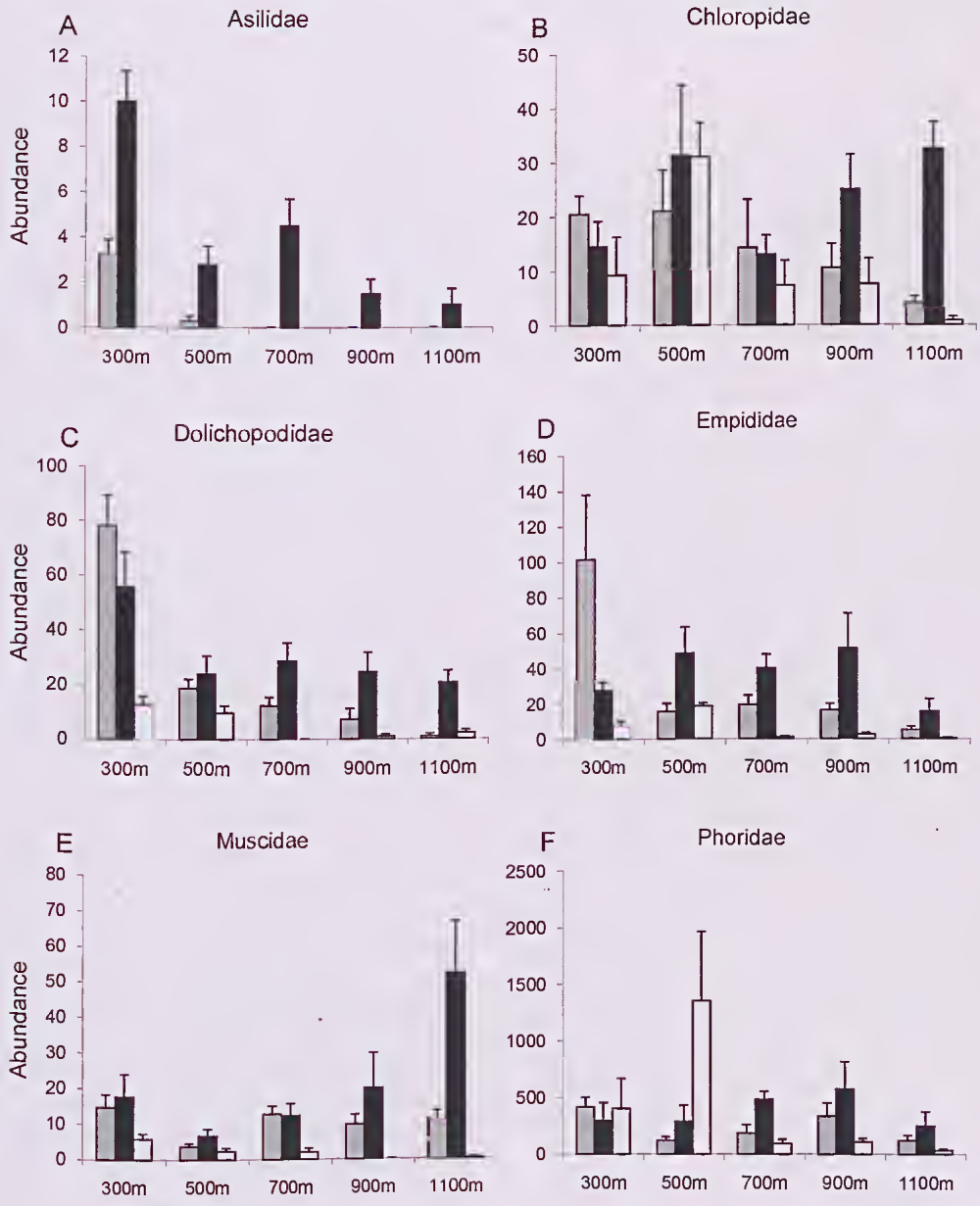


FIG. 6. Mean (+SE) abundances of the six fly families that were included in the three subsets of families selected by the Bio-Env procedure (see Results). A, Asilidae; B, Chloropidae; C, Dolichopodidae; D, Empididae; E, Muscidae; F, Phoridae.

extremes of altitude, that is the highest and lowest altitudes, tend to be most consistently different from other altitudes.

Seven brachyceran families were the most abundant; the Phoridae, Empididae, Dolichopodidae, Chloropidae, Drosophilidae, Sphaeroceridae, and Muscidae. The dominance of these families is consistent with an earlier study at Lamington National Park which also used Malaise trap samples and found the same seven families dominated the brachyceran fauna (Kitching *et al.* 2004).

The overall seasonal pattern of dipteran abundance is also consistent with those found for other surveys of tropical insects (e.g. Frith & Frith 1985; Wilson *et al.* 2007a) with flies at their most abundant in summer and lowest in winter. However, not all families followed this trend. For example, the Rhagionidae, Ephydridae, Heleomyzidae, Lauxanidae, Milichiidae and Sphaeroceridae were most abundant in October, possibly reflecting Spring emergences, and winter active families included the Phoridae, Chloropidae and Drosophilidae. In each of these three families, aspects of their feeding biology or habit may facilitate their success under cooler conditions. In a study of flies in subtropical rainforests, Kitching *et al.* (2005) similarly found that the schizophoran families Chloropidae, Lauxaniidae, Heliomyzidae, and Ephydridae increased in numbers during winter. Since the majority of species in these families are not predators or fully aquatic decomposers, Kitching *et al.* (2005) suggested their resource base was maintained through the dry cooler season. In the Wet Tropics, schizophoran flies are most abundant in Spring (October) at higher altitudes and in autumn (April) at lower altitudes (Wilson *et al.* 2007a). While we have not sorted the autumn sample (March), we observed the same trend at higher altitudes.

While the change was less consistent than that demonstrated between seasons, fly family assemblages do change across the altitudinal gradient. The majority of fly families (33 out of 46) were most abundant at the two lowest altitudes, however the Sciadoceridae, Calliphoridae, Clusiidae, Ephydridae, Helosciomyzidae, Lauxaniidae and Muscidae were most abundant in the 1100 m samples (Table 1). Our analysis indicated that the Asilidae, Dolichopodidae, Chloropidae, Muscidae, Phoridae, and Empididae contributed most to the pattern of fly assemblages between altitudes being expressed differently across the three seasons. Each family is likely to respond to the environmental conditions in accordance with their habit or life cycle needs. There were some consistent patterns across families. For example, the predatory groups, the Dolichopodidae, Empididae and Asilidae, showed a general pattern of decreasing abundance with increasing altitude, with abundances highest in summer and lowest in winter, with Asilidae completely absent from the winter sample. Available data suggest that predation by insects decreases with increasing altitude (Hodkinson 2005). This pattern may be directly related to the decrease in prey abundance with increasing altitude. In addition, the searching efficiency of these active predators may be impaired under the cooler and often misty conditions at the higher altitudes, as has been seen in parasitoids (Coulson *et al.* 1995). Other families showed different responses to altitude across seasons. For example, the Phoridae were most common in winter, with a peak in abundance at 500 m and lowest numbers at 1100 m. While the high abundance of Phoridae in winter might indicate an ability to cope with cooler conditions, their peak abundance at 500 m and decline at 1100m shows that these decomposers of terrestrial organic matter avoid the extremes of that season by occupying warmer, moister habitats.

The upper and lower distributional limits of a species are determined by its capacity to match its thermal tolerance range to the temperature profile of its habitat (Hodkinson *et al.* 1999). With temporal variation in temperature, the upper distributional limits of species may fluctuate on a seasonal basis (Hodkinson 2005). For example, Menendez &

Gutierrez (2004) demonstrated that seasonal shifts in the distribution of species of dung beetles are linked to corresponding shifts in microclimatic conditions. The presence of any fly family at a particular altitude in a particular season is likely to reflect environmental determinants of the distribution of individual taxa within that family. For example, the presence of particular families at lower, warmer altitudes in winter and higher, cooler altitudes in summer reflects species of these families occupying the most suitable habitat throughout the year. Future research should focus on the responses of individual species and whether they also display seasonal shifts in distribution and abundance across altitude. Vegetation, humidity, rainfall, minimum and maximum temperatures, available sunlight, soil temperature, moisture and chemical composition change considerably across the IBISCA-Queensland gradient (see Strong *et al.* 2011). Any of these parameters have the potential to influence the composition and abundances of fly families through effects on the environmental requirements of immatures and adults.

CONCLUSIONS

The results of this study highlight the complex responses of the ubiquitous Diptera to changes in environmental conditions. While changing altitude, and accompanying changes in microclimate, was expected to have a pronounced effect on fly assemblages, mirroring responses expected due to future climate change, the influence of altitude was overwhelmed by seasonal variation in climate. The differential pattern observed among families gives some indication of the range of possible responses to climate change – beyond simple decreasers and increasers. Further information on responses of individual species to altitude and season is likely to greatly improve our understanding of the complexity of the patterns oberserved here. Future studies should focus on whether there are seasonal shifts in the distribution and abundance of individual species across altitude.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We would like to give particular thanks to the field efforts of Kyran Staunton, Geoff Monteith, and the volunteers John Gray and Stefan Curtis. We also acknowledge the image enhancement and preparation of figures by Geoff Thompson, Queensland Museum. We would also like to thank Shane McEvey (Australian Museum, Sydney), Jeffrey Skevington (Canadian National Collection, Ottowa), and Rohan Wilson (Australian National University, Canberra) for all their work on species-level identifications for an earlier version of this paper. C.L.L. and N.T.S. were supported by funding from the Queensland Museum. S.L.B was the grateful recipient of an APA scholarship and Smart State top-up scholarship during the preparation of this manuscript.

LITERATURE CITED

Anderson M.J., Gorley R.N. & Clarke K.R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* (PRIMER-E: Plymouth).

Arroyo, M.T., Primack, R. & Armesto, J.J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany* 69: 82-97.

Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P. & Chown, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.

Brehm, G., Colwell, R.K. & Kluge, J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* **16**: 205-219.

Brehm, G. & Fiedler, K. 2003. Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography* **30**: 431-440.

Bruhl, C.A., Mohamed, V. & Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15**: 265-277.

Chatzaki, M., Lymberakis, P., Markakis, G. & Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography* **32**: 813-831.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117-143.

Clarke, K.R. & Gorley, R.N. 2006. *PRIMER v6: User Manual/Tutorial*. (PRIMER-E: Plymouth).

Coulson, S.J., Hodkinson, I.D., Strathdee, A.T., Block, W., Webb, N.R., Bale, J.S. & Worland, M.R. 1995. Thermal environments of Arctic soil organisms during winter. *Arctic and Alpine Research* **27**: 365-371.

Darling, D.C. & Packer, L. 1988. Effectiveness of malaise traps in collecting Hymenoptera: the influence of trap design, mesh size and location. *Canadian Entomologist* **120**: 787-796.

Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other Arthropod species. The *Coleopterists Bulletin* **36**: 74-75.

Escobar, F., Lobo, J.M. & Halffter, G. 2005. Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Global Ecology and Biogeography* **14**: 327-337.

Evans, F.C. & Owen, D.F. 1965. Measuring insect flight activity with a malaise trap. *Papers of the Michigan Academy of Science, Arts and Letters* **50**: 89-94.

Fisher, B.L. 1996. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andringitra, Madagascar. *Fieldiana Zoology* **85**: 93-108.

Fisher, B.L. 1999. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zoology* **94**: 129-147.

Fleishman, E., Fay, J.P. & Murphy, D.D. 2000. Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *Journal of Biogeography* **27**: 1209-1219.

Frith, C.B. & Frith, D.W. 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* **10**: 237-248.

Hamilton, J., Yeates, D., Hastings, A., Colless, D., McAlpine, D., Bickel, D., Daniels, G., Schneider, M., Cranston, P. & Marshall, S. 2006. *On The Fly: The Interactive Atlas and Key to Australia Fly Families*. (Australian Biological Resources Study, Canberra & Centre for Biological Information Technology: St. Lucia).

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**: 489-513.

Hodkinson, I.D., Bird, J.M., Miles, J.E., Bale, J.S. & Lennon, J.J. 1999. Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology* **13**: 83-95.

Kearns, C.A. 1992. Anthophilous fly distribution across an elevation gradient. *American Midland Naturalist* **127**: 172-182.

Kitching, R.L., Bickel, D. & Boulter, S. 2005. Guild analyses of Dipteran assemblages: a rationale and investigation of seasonality and stratification in selected rainforest faunas. Pp 388-415. *In*, Yeates, D.K. & Wiegmann, B.M. (eds), *The evolutionary biology of flies*. (Columbia University Press: New York).

Kitching, R.L., Bickel, D., Creagh, A.C., Hurley, K. & Symonds, C. 2004. The biodiversity of Diptera in Old World rain forest surveys: a comparative faunistic analysis. *Journal of Biogeography* **31**: 1185-1200.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55**(2): 271-290.

Lambkin, C.L., Power, N. & Starick, N.T. 2002. Mt Kosciuszko: Biodiversity of Flies (Diptera). Pp 76-87. *In*, Green, K. (ed.), *Biodiversity in the Snowy Mountains*. (Australian Institute of Alpine Studies: Jindabyne).

Malaise, R. 1937. A new insect-trap. *Entomologisk Tidskrift* **58**: 149-160.

McKie, B.G., Pearson, R.G. & Cranston, P.S. 2005. Does biogeographical history matter? Diversity and distribution of lotic midges (Diptera: Chironomidae) in the Australian Wet Tropics. *Austral Ecology* **30**: 1-13.

Menendez, R. & Gutierrez, D. 2004. Shifts in habitat associations of dung beetles in northern Spain: Climate change implications. *Ecoscience* **11**: 329-337.

Monteith, G.B. & Davies, V.T. 1991. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp 345-362. *In*, Werren, G. & Kershaw, P. (eds), *The Rainforest Legacy: Australian National Rainforest Study*. (Australian Government Publishing Service: Canberra).

Novotny, V. & Basset, Y. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* **89**: 564-572.

Power, N. 1998. *Temporal and spatial diversity of Therevidae in South East Queensland (Diptera: Therevidae)*. Honours Thesis. (Department of Entomology, University of Queensland: Brisbane).

Sanders, N.J., Lessard, J.-P., Fitzpatrick, M.C. & Dunn, R.R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* **16**: 640-649.

Southwood, T.R.E. 1978. *Ecological methods with particular reference to the study of insect populations*. 524 Pp. (Chapman and Hall: London).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Townes, H. 1962. Design for a Malaise trap. *Proceedings of the Entomological Society of Washington* **64**: 253-262.

Townes, H. 1972. A light-weight Malaise trap. *Entomological News* **83**: 239-247.

Warren, S.D., Harper, K.T. & Booth, G.M. 1988. Elevational distribution of insect pollinators. *American Midland Naturalist* **120**: 325-330.

Wilson, R.D., Trueman, J.W.H., Williams, S.E. & Yeates, D.K. 2007a. Altitudinally restricted communities of schizophoran flies in Queensland's Wet Tropics: vulnerability to climate change. *Biodiversity and Conservation* **16**: 3163-3177.

Wilson, R.J., Gutierrez, D., Gutierrez, J. & Monserrat, V.J. 2007b. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**: 1873-1887.

Yeates, D.K. 1985. Altitudinal transect studies at Cape Tribulation, north Queensland IV. The march flies (Diptera: Tabanidae). *Queensland Naturalist* **26**: 58-61.

Yeates, D.K., Bickel, D., McAlpine, D.K. & Colless, D.H. 2009. Diversity, relationships and biogeography of Australian flies. Pp 227-256. *In*, Pape, T., Bickel, D. & Meier, R. (eds), *Diptera Diversity. Status, challenges and tools*. (Koninklijke Brill NV: The Netherlands).

Potential effects of climatic warming on the distribution of Collembola along an altitudinal transect in Lamington National Park, Queensland, Australia

Penelope GREENSLADE

School of Biology, Australian National University, Canberra ACT 0200, Australia and Centre of Environmental Management, School of Science, Information Technology and Engineering, University of Ballarat, PO Box 663 Ballarat Vic 3353, Australia. Email: pgreenslade@staff.ballarat.edu.au

Roger L. KITCHING

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia.

Citation: Greenslade, P. & Kitching, R.L. 2011 12 20: Potential effects of climatic warming on the distribution of Collembola along an altitudinal transect in Lamington National Park, Queensland, Australia. *Memoirs of the Queensland Museum – Nature* 55(2): 333-347. Brisbane. ISSN 0079-8835.

ABSTRACT

Collembola were collected from pitfall traps at each of five altitudes, 300, 500, 700, 900 and 1100 m above sea level (a.s.l.) in Lamington National Park, Queensland. All samples were collected in October 2006 (spring). Sites were located in subtropical rainforest except for those at 1100 m which were in cool temperate rainforest where *Nothofagus moorei* (F. Muell) Krasser was dominant. Specimens collected were identified to species or morphospecies. Over 60 taxa (species and morphospecies) were identified from more than 7000 specimens. Species assemblages were significantly related to altitude generally showing a progressive change in composition with increasing altitude. Assemblages at the highest altitude of 1100 m were particularly distinct and several taxa were restricted to this altitude. Altitudinal patterns of assemblages of Collembola are compared with those of some other invertebrates from the same transect and suggestions for the differences offered. A review of altitudinal zonation in Collembola in various regions and climatic zones is provided. ❐ *Nothofagus, rainforest, montane faunas, altitudinal zonation, Paronellidae, Entomobryidae, Odontellidae, Symphypleona, Isotomidae, Hypogastruridae, IBISCA*

It is now generally accepted that global warming is accelerating and has the potential to alter considerably the distribution of both biological communities and their component species. If we are to conserve biological diversity and the ecosystem services it provides, we first need to document the possible effect of climate change on vulnerable faunal assemblages. This will not only improve understanding of the potential for natural processes of adaptation to occur (or not, as the case may be) but also to identify target organisms for monitoring such changes.

The IBISCA (Investigating the Biodiversity of Soil & Canopy Arthropods)-Queensland (Qld) project at Lamington National Park aimed to sample fauna and flora along a transect of increasing altitude to provide baseline data on species' distributions as temperature

decreases and rainfall increases (Kitching *et al.* 2011). From this baseline information, we can recognise species or other taxa that have limited ranges along the transect. The overall aim of the project was to identify taxa that are 'climate responders' so that they can be monitored on a regular basis using focused sampling strategies. Any alterations in distribution of these taxa over time could be detected by monitoring, unless they are very rare. In an otherwise largely undisturbed environment the change may be assumed to be the result of climate variation, if the direction of the altered change is the same as that predicted to occur as a result of climate change. Of course, such monitoring needs to occur on a regular basis over a long enough time scale to overcome the impacts of short-term climatic variability. Data on indicator taxa could feed into management decisions in subtropical regions and become key components of monitoring/management systems. A considerable number of taxa have been surveyed within this project and Collembola (springtails) were one target group. Springtails are particularly suitable for including in such a study as they are abundant and species-rich in the Lamington National Park (Rodgers & Kitching 1998, 2010). Collembola can also be quickly and easily collected using a range of methods.

The collembolan fauna of subtropical forest is little known in Australia, or indeed anywhere in the world. To date, only ten named species of Collembola have been recorded in the published literature from Lamington National Park (Greenslade & Sutrisno 1994; Rodgers & Kitching 2010) and 24 species of Entomobryidae, mainly unidentified, were recorded from the canopy at 700 m above sea level (a.s.l.) in an unpublished thesis (Sutrisno 1994). The same is true of altitudinal zonation of collembolan faunas in general and only a few studies have been conducted of ground-living Collembola (Leakey & Proctor 1987; Bedos 1994; Gabriel *et al.* 2001; Greenslade 2004), none of these being in subtropical climes. Relevant data from these studies has been compared to the Lamington results reported here.

Here, the composition and other characteristics of the collembolan fauna at the different altitudes, sampled for the IBISCA-Qld project in pitfalls on a single occasion, are documented and the wider implications of these findings discussed in relation to species at risk of extinction under a hotter, drier climatic regime. Based on data from other invertebrate taxa, the hypotheses to be tested by the IBISCA-Qld project will be that different assemblages of species occur at different altitudes and that abundance and species richness diminishes as altitude increases.

MATERIALS AND METHODS

The trapping programme formed the basis of the IBISCA-Queensland project in the subtropical rainforest of Lamington National Park and used consistent and repeatable collecting methods in 20 plots at five altitudes; four replicates per altitude (see Kitching *et al.* 2011). The plots are permanently marked and cover altitudes from 300 to 1100 m a.s.l. at intervals of two hundred metres (Laidlaw *et al.* 2011). A brief description of the vegetation at each alititude is given in Table 1. Altogether, this project used seven baseline sampling methods in three major sampling events (October 2006, March 2007 and January 2008) (Kitching *et al.* 2011). All methods collected Collembola but only samples from pitfall traps set in October 2006 are reported here.

At each of the 20 plots, an array of nine pitfalls were set and left in the ground for nine days. They were arranged in a cross grid with each trap being a minimum of one metre from the nearest one. Traps were 50 mm in diameter (a 120 ml plastic vial within a PVC sleeve) with an aperture diameter of 43 mm and filled with 70% ethanol. Catches from the nine traps were combined before sorting. Collembola were identified to species or morphospecies and counted. All specimens have been deposited in

TABLE 1. Vegetation type and dominant plant species present for each altitude sampled along the transect in Lamington National Park. *From Sattler *et al.*, 1999.

Altitude (m a.s.l.)	Regional Ecosystem*	Description
300	12.8.4	Complex notophyll vine forest on Caenozoic igneous rocks with *Araucaria cunninghamii, Argyrodendron actinophyllum, Baloghia inophylla, Brachychiton acerifolius, Dendrocnide excelsa, Diospyros pentamera, Dysoxylum fraserianum, Toona ciliata* and *Orites excelsus.*
500	12.8.3	Complex notophyll vine forest on Caenozoic igneous rocks with *Argyrodendron trifoliolatum, Olea paniculata, Castanospermum australe, Cryptocarya obovata, Ficus macrophylla, Syzygium francisii, Diploglottis australis, Pseudoweinmannia lachnocarpa, Podocarpus elatus, Beilschmiedia obtusifolia, Neolitsea dealbata* and *Archontophoenix cunninghamiana.*
700 and 900	12.85	Complex notophyll vine forest on Caenozoic igneous rocks with *Argyrodendron actinophyllum, Cryptopcarya erythroxylon, Ficus watkinsiana, Dysoxylum fraserianum, Caldcluvia paniculosa, Geissois benthamii, Orites excelsus, Acmena ingens, Syzygium corymanthum, S. crebrinerve* and *Citronella moorei.*
1100	12.8.5	Simple microphyll fern forest on Caenozoic igneous rocks with *Nothofagus moorei* and/or *Doryphora sassafras, Caldcluvia paniculosa* and *Orites excelsus.*

the South Australian Museum and a voucher collection at the Arthropod Biodiversity Laboratory, Griffith University, Nathan. Some species have been bar-coded (Bar-coding of Life Project).

Average temperatures at the sites range from 18°C at 300 m a.s.l. to 15°C at 1100 m a.s.l. Average maxima and minima temperatures range from 28°C to 5°C, being highest at lowest altitudes. Total annual rainfall is around 1200 mm at 300 m a.s.l. and increases gradually with altitude to around 2400 mm at 1100 m a.s.l. (Australian Government, Bureau of Meteorology 2008). A set of environmental variables was assembled from data presented in other papers within this volume (Laidlaw *et al.* 2011; Strong *et al.* 2011). For each plot, this set included data on vegetation (basal area, number of stems, plant species richness), climate (minimum temperature, median temperature, maximum temperature and atmospheric moisture), soils (moisture, pH, organic content, NO_3, P, K, and Ca) and volume of decaying timber (standing and fallen).

Relationships between the composition of collembolan assemblages from each plot were examined using non-metric multidimensional scaling (NMDS) ordination using Bray-Curtis similarity values of species and morphospecies abundance (log transformed) data. PERMANOVA (permutational multivariate ANOVA, Anderson *et al.* 2008) was conducted to statistically investigate the effect of altitude on collembolan assemblage composition. PERMANOVA is analogous to traditional multivariate ANOVA, except that it calculates statistics (pseudo-*F* values) from distance measures of assemblage similarities between sites, and *P* values using permutational techniques (we used 999 permutations). Post-hoc pairwise comparisons were also conducted using 999 Monte-Carlo permutations between altitudes. Vectors of environmental variables were fitted onto the NMDS ordination. The direction of each vector represents the gradient of the environmental variable and its length is proportional to the correlation between the ordination and environmental variable. Only environmental variables with significant correlation coefficients (at a significance level of $P<0.05$ based on 999 random permutations) were overlaid on the ordination. Analyses were performed using PRIMER 6 (Clarke & Gorley 2006).

A similar transect across an altitudinal gradient was sampled for Collembola with pitfall traps in southern Tasmania (Grove *et al.* 2004; Greenslade 2004). Some data from this transect has been included for comparison with the Lamington data to compare latitudinal differences in zonation.

RESULTS

Over 60 collembolan taxa at the species and morphospecies levels were identified from more than 7000 specimens (Table 2). Species richness and abundance increased with altitude to 900 m but then fell at 1100 m (Table 3). However, the number of families trapped at each altitude did not differ markedly. The contribution that each family made to the total numbers of individuals trapped at different altitudes varied (Fig. 1, Table 4). The most abundant families trapped were the Paronellidae and Entomobryidae and the Paronellidae was more abundant at the lowest altitude. Families Odontellidae, Hypogastruridae and Dicyrtomidae were most abundant in traps at the highest altitude, and the Isotomidae and Neanuridae were most abundant at both 900 and 1100 m. Other families tended to be most abundant at 900 m, including the Entomobryidae, Katiannidae and Sminthuridae. Sminthurididae were not trapped above 700 m. Other families did not show a strong pattern of distribution or were present in insufficient numbers for the data to be meaningful.

The numerically dominant paronellid was *Pseudoparonella queenslandica* Schött, and in the Entomobryidae was *Acanthocyrtus spinosus* Schött, both fairly widespread species in eastern Australia and common along the entire altitudinal transect, although less abundant at 1100 m (Table 2). Other species showed some altitudinal restrictions (Table 2). *Epimetrura rostrata* Sutrisno and Greenslade (Entomobryidae) was found exclusively, but in small numbers, at 700 m. It has previously been shown to be abundant in the canopy at this altitude where it was found to comprise nearly 60% of total Collembola (Sutrisno 1994). Two species belonging to two different isotomid genera showed different and sequential preferences as regards altitude. A species belonging to the *Cryptopygus antarcticus* Willem group was found most abundantly at 1100 m and rarely at 900 m while a species of *Isotopenola* was found at 700 and 900 m only. The only tomocerid species, a member of the southern genus *Lepidophorella*, was found commonly along the transect but mainly at mid-altitudes. In the frequent but not abundant Symphypleona, a small number of specimens of a species of the rare genus *Adelphoderia* was found only at 500 m. Members of the leaf litter inhabiting Katianninae were more frequent and abundant at 900 m, while the epigaeic *Rastriopes* and *Sphyrotheca* in the Bourletiellidae were more abundant at the lower altitudes. Apart from a rare *Xenylla* species, the Hypogastruridae was represented only by a species of *Triacanthella*, not entirely restricted to but more frequent and abundant at 900 and 1100 m. It should be noted that as only pitfall collections are reported here, rare species in these collections could indicate that the species is not active on the ground surface but may be more common in a soil habitat for instance. The humidity-loving Odontellidae were represented by several species at high altitude and the single species of the Uchidanurinae (*Acanthanura* sp., Neanuridae), an endangered subfamily in Australia (Greenslade 1991a), was trapped only at 1100 m in the *Nothofagus* forest.

We identified five 'sentinel' species (Table 5), represented by multiple specimens collected from only a single elevation, that are promising candidates for future monitoring of climate change; *Pseudachorutinae* sp. 2 and *Acanthanura* sp. (both Neanuridae) restricted to 1100 m a.s.l., *Pseudachorutinae* sp. 1 (Neanuridae) only at 900 m, *Adelphoderia* sp. (Katiannidae) only at 500 m, *Rastriopes* sp. 2 (Bourletiellidae) only at 300 m.

The ordination grouped the plots at 1100 m into a tight and well-separated cluster but

TABLE 2. List of Collembola taxa collected in pitfall traps along the IBISCA-Qld transect and total numbers of individuals trapped at each altitude (summed across four replicate plots) with an estimate of preferred altitude for selected taxa (*300 m, **500 m, ***700 m, **** 900 m, *****1100 m) (brackets denote a weaker response at the altitude they enclose).

	300	500	700	900	1100	Preferred Altitude
ARTHROPLEONA (Poduromorpha)						
Neanuridae						
Acanthanura sp.	0	0	0	0	4	*****
Ceratrimeria sp.	1	0	2	23	0	****
Pseudachorutinae sp. 1	0	0	0	2	0	****
Pseudachorutinae sp. 2	0	0	0	0	6	*****
Pseudachorutinae sp. 3	2	1	1	0	12	*****
Neanurinae Lobellini	0	0	0	2	0	****
Paleonura sp.	0	0	0	0	2	*****
Odontellidae						
Indeterminate spp.	0	1	36	33	96	**(**)*
Brachystomellidae						
Brachystomella sp.	1	0	0	0	0	unclear
Hypogastruridae						
Triacanthella sp.	0	0	3	11	23	***(*)*
Xenylla sp.	2	0	0	2	0	unclear
ARTHROPLEONA						
Isotomidae						
cf. *Folsomina* sp.	0	0	0	0	2	*****
Cryptopygus antarcticus grp	0	0	0	2	14	***(*)*
Proisotoma sp.	0	0	0	0	1	unclear
Isotopenola sp.	0	0	8	12	0	**(*)*
cf. *Parisotoma*	0	0	0	2	2	****(*)
Isotoma tridentifiera	12	0	4	32	5	widespread
Acanthomurus sp. 1	0	0	0	6	19	(*)****
Acanthomurus sp. 2	0	0	0	0	2	*****
Tomoceridae						
Lepidophorella sp.	0	13	30	20	5	*(*)**
Entomobryidae						
Lepidocyrtoides sp. 1	31	51	45	1	12	widespread
Lepidocyrtoides sp. 2	75	24	11	63	4	widespread
Epimetrura rostrata	0	0	0	20	0	****
?*Acanthocyrtus* sp. 1	151	64	90	208	1	absent 1100
Entomobryidae sp. 1	221	116	12	0	3	*(*)
Entomobrya sp. cf. *virgata*	1	0	8	3	2	widespread

TABLE 2. cont...

	300	500	700	900	1100	Preferred Altitude
Entomobrya varia	19	8	9	5	0	absent 1100
?*Sinella* sp.	1	1	7	12	11	unclear
Discocyrtus sp. cf. *cinctus*	0	1	59	213	71	****(*)
Lepidocyrtus sp. 1	4	126	47	90	0	absent 1100
Lepidocyrtus sp. 2	33	63	27	164	0	absent 1100
Lepidocyrtini sp. 3	13	38	65	14	6	widespread
Acanthocyrtus sp. 2	40	2	127	141	0	absent 1100
Indet. sp. 2	0	0	0	1	0	unclear
Immature Entomobryidae	216	133	338	208	22	
Paronellidae						
Pseudoparonella queenslandica	681	244	90	220	40	*
Paronellides sp.	0	0	0	5	0	****
Paronellidae sp. 1	19	29	55	68	48	widespread
Paronellidae sp. 2	5	58	39	42	30	widespread
Paronellidae sp. 3	0	55	24	12	9	widespread
Paronellidae sp. 4	0	1	1	2	0	widespread
Salina sp.	0	0	1	0	0	unclear
Immature Paronellidae	152	162	163	82	108	
SYMPHYPLEONA						
Immature Symphypleona	8	11	0	17	0	
Sminthurididae						
Sphaeridia sp.	5	0	6	0	0	widespread
Katiannidae						
Arrhopalites sp.	0	0	1	0	0	unclear
Adelphoderia sp.	0	3	0	0	0	**
Smintlurinus sp.	5	1	0	4	3	widespread
Smintlurinus sp.	0	1	0	0	2	unclear
Katianna sp. 1	0	2	1	138	33	****
Katianna sp. 2	0	1	4	0	10	widespread
Katianninae sp. 1	36	0	8	65	12	widespread
Katianninae sp. 2	0	1	0	1	4	*****
Immature Katiannidae	13	0	37	28	21	
Sminthuridae						
Temeritas sp. 1	1	0	29	3	2	***
Temeritas sp. 2	0	0	0	1	0	unclear
Sphyrotheca sp.	10	59	10	33	9	widespread

TABLE 2. cont...

	300	500	700	900	1100	Preferred Altitude
Pararrhpalites sp.	0	1	0	0	0	unclear
Bourletiellidae						
Bourletiellidae gen. indet. 1	2	0	0	1	2	widespread
Bourletiellidae gen. indet. 2	4	1	0	0	0	*
Rastriopes sp. 1	0	0	0	0	1	*
Rastriopes sp. 2	3	0	0	0	0	*
Dicyrtomidae						
Dicyrtomidae sp. 1	0	17	7	3	70	widespread
Dicyrtomidae sp. 2	0	1	0	23	0	****
cf.? *Calvatomina pagoda*	0	0	0	0	1	*****
Total Individuals	1767	1290	1405	2038	730	

TABLE 3. Numbers of species and individuals (abundance) of Collembola at each elevation along the IBISCA-Qld transect, Lamington National Park, and along transects at Warra (100–600 m a.s.l.) and Mt Weld (600–1300 m a.s.l.) in southern Tasmania.

	Elevation (a.s.l.) in metres												
Number of species	100	200	300	400	500	600	700	800	900	1000	1100	1200	1300
Lamington	-	-	31	-	33	-	34	-	44	-	40	-	-
Warra	22	21	17	23	20	15	-	-	-	-	-	-	-
Mt Weld	-	-	-	-	-	12	19	21	26	20	22	14	11
Abundance													
Lamington	-	-	1767	-	1290	-	1176	-	2038	-	730	-	-
Warra	329	299	277	302	148	121	-	-	-	-	-	-	-
Mt Weld	-	-	-	-	-	40	300	721	999	378	1522	532	520

the remainder of the plots showed less distinct groupings, in that assemblage composition tended to gradually change from low to high elevation (Fig. 2). PERMANOVA showed that altitude significantly influenced assemblage composition (pseudo-F = 4.34, $p<0.01$), with pairwise post-hoc comparisons showing significant differences between all pairs of altitudes except for 500 and 700 m and 700 and 900 m. The fitted vectors indicate the environmental factors that are significantly correlated with the ordination of collembolan assemblages (Fig. 2). Environmental factors positively correlated with the assemblages from higher altitudes were soil moisture, soil organic content, atmospheric moisture (all $p<0.01$) and soil nitrite concentration ($p<0.05$). Those correlated with assemblages from lower altitudes were tree species richness, high temperature, median temperature, higher soil pH, soil calcium levels, soil potassium (all $p<0.01$) and minimum temperature ($p<0.05$).

TABLE 4. Total abundance, individuals collected in pitfall traps, of each family of Collembola across the whole IBISCA-Qld transect and at each elevation at Lamington National Park.

	Altitude (m a.s.l.)					
Family	300	500	700	900	1100	Total
Neanuridae	3	1	3	27	24	58
Odontellidae	0	1	36	33	96	166
Brachystomellidae	1	0	0	0	0	1
Hypogastruridae	2	0	3	13	23	41
Isotomidae	12	0	12	54	45	123
Tomoceridae	0	13	30	20	5	68
Entomobryidae	805	627	845	1142	132	3551
Paronellidae	857	719	373	431	220	2600
Sminthurididae	5	9	6	0	0	20
Katiannidae	54	60	51	236	85	486
Sminthuridae	11	12	0	37	11	71
Bourletiellidae	17	18	7	18	3	63
Dicyrtomidae	0	18	7	26	71	122

DISCUSSION

Generalities suggested by the data presented here must be viewed with caution since they relate to one moment in time (October 2006) and are from pitfall catches only, so represent only the fauna active on the ground surface. Even so, they demonstrate some changes in collembolan assemblage composition with altitude. At the highest altitude (1100 m) showed a clear divergence in species composition compared with the other plots, there was a gradual trend along the altitude gradient of the collembolan assemblages towards 1100 m and few species were found at all altitudes. In addition, there was a change in family abundance with altitude. In support of these results, Maunsell (2009), comparing leaf litter faunas at the 700, 900 and 1100 m IBISCA-Qld plots, also found that the Collembola assemblage at 1100 m was distinctly different from the other two altitudes. Some altitudinal changes in numbers of individuals trapped, species richness and species distributions were also evident in this and Maunsell's (2009) study.

Of the few altitudinal studies that have been completed in Australia for Collembola, those at Warra and Mt Weld in Tasmania (Greenslade 2004) are the most relevant (Tables 3, 6, 7) and some altitudinal trends are also evident here. Lowest species richness and individuals trapped appeared to be at the mid-altitudes of 500 and 600 m (Table 3). This trend is not evident in the Lamington data. One similarity between the two latitudes is that of family distribution with the highest abundance of Isotomidae in traps in the Tasmanian study also being found at altitudes greater than 900 m (Table 7). Neanuridae and Odontellidae were also most abundant at high altitude in traps at 800 m, but not at 900 m probably because, unlike at Lamington, alpine vegetation, and not forest, was present at 900 m in Tasmania. However, differences in family distribution between the Queensland and Tasmanian sites are evident with Paronellidae being abundant at altitudes of 1200 and 1300 m on Mt Weld (Table 7) but being most abundant at the lowest altitudes (300 and 500 m) at Lamington. The effects of climate warming at the two latitudes are likely to lead to changes in family signatures at the different altitudes.

References to data from transects elsewhere are listed in Table 6. On two mountains in Tasmania and two in New Zealand, Andrew *et al.* (2003), using a flotation method of extraction from soil, found a decrease in invertebrate richness, including Collembola, with altitude and no change in abundance, these authors only identified invertebrates to family. In Sabah, Leakey and Proctor (1987) found a reduction in abundance of litter Collembola with increasing altitude but no change in soil Collembola, but these authors only used hand collections. Altitudinal studies from the Solomon Islands comparing coastal, forest and montane soil and leaf litter collembolan faunas found, as at Lamington and in Tasmania, a lower abundance

TABLE 5. List of Collembola 'climatic predictors', the elevation at which they currently occur and prediction of future changes under climate warming. * Only one specimen collected.

Species	Current distribution (m)	Possible change
Acanthaunura sp.	1100	Local extinction
Pseudachorutinae sp. 1	900	Only at 1100 m
Pseudachorutinae sp. 2	1100	Local extinction
Odontellidae	500–1100	Eliminated from 500 m
Triacanthella sp.	700–1100	Eliminated from 700 m
Cryptopygus antarcticus grp	900–1100	Only at 1100 m
Isotopenola sp.	700–900	Eliminated from 700 m
Adelphoderia sp.	500	Local extinction
Rastriopes sp. 1	1100	Local extinction*
Rastriopes sp. 2	300	Elevation to 500 m
Sphyrotheca sp.	300–900	Extinction at 300 m

TABLE 6. Published data on species richness and abundance of Collembola with altitude.

Author/year sampled	Location	Altitudinal range (m a.s.l.)	Sampling method	Trends in abundance with increasing altitude	Trends in species richness with increasing altitude
This work/2006	Lamington NP, Queensland, Australia	300–1100	Pitfalls	Decrease at 1100m only	Increase
Greenslade/1965	Popamanusiu, Solomon Islands	ca.1000–1800	Tullgren funnel of leaf litter and soil	Decrease	Decrease
Bedos/1981–92	Don Inthanon, Thailand	>1000–2500	Tullgren funnel of leaf litter and soil	Rather higher	Rather higher
Leakey & Proctor/1983	Gunung Silam, Sabah, Malaysia	280-870	Hand sorting	Decrease in leaf litter fauna, no change in soil fauna	Not identified beyond Class
Andrew *et al.*/1996	Tasmania and New Zealand	250–1250 (Tas.) 650–2000 (NZ)	Flotation using kerosene	No change	Sometimes decrease in family richness but varied with mountain and country
Gabriel *et al.*/1996–99	Marion Island	50-1270	Tullgren funnel of soil	Not documented	Exotic species at lower elevation, native species at higher elevation
Greenslade/2001–2	Warra,Tasmania, Australia	100–600	Pitfalls and Malaise traps	Decrease	Decrease
Greenslade/2001–2	Mt Weld, Tasmania, Australia	600–1300	Pitfalls and Malaise traps	Decrease	Decrease

TABLE 7. Family signatures (numbers of individuals trapped in each family) for Collembola collected along altitudinal transects at Warra and Mt Weld, Tasmania.

Altitude (m a.s.l.)	Family											
	Bourletiellidae	Brachystomellidae	Dicyrtomidae	Entomobryidae	Isotomidae	Katiannidae	Neanuridae	Odontellidae	Paronellidae	Indet. poduromorphs	Indet. Symphypleona	Tomoceridae
Warra												
100 m	0	0	37	159	1	13	37	2	21	8	49	2
200 m	0	2	78	76	27	2	63	0	13	17	19	2
300 m	0	3	118	31	34	1	16	1	37	23	10	3
400 m	0	53	0	48	23	58	33	14	54	9	8	25
500 m	0	10	0	27	20	12	24	0	11	12	22	10
600 m	0	2	0	12	38	19	22	1	5	11	0	11
Mt Weld												
600 m	0	1	6	4	16	2	7	1	1	0	2	0
700 m	0	1	0	106	71	4	75	1	12	19	0	11
800 m	3	3	0	190	150	0	131	134	3	57	45	4
900 m	3	0	7	51	658	11	65	54	12	47	74	17
1000 m	9	1	9	37	153	6	35	0	46	11	61	10
1100 m	13	1	1	18	1324	2	3	0	16	5	137	2
1200 m	0	0	0	22	237	58	0	18	130	0	65	2
1300 m	0	0	0	10	326	16	3	56	109	0	0	0

of Collembola at montane sites (P. Greenslade unpub. data). The fauna at high altitude on Mount Popamanusiu in the Solomon Islands, at about 1800 m, lacked Symphypleona and Paronellidae and the proportion of Isotomidae and Tullbergiidae increased. No Tullbergiidae were found at Lamington or in Tasmania, but members of this family do not readily fall into pitfalls as they are soil-inhabiting. In fact, Isotomidae were best represented at the two highest altitudes both in the Solomons, at Lamington and in Tasmania.

The most comprehensive study of altitudinal zonation of Collembola was conducted in tropical rainforest on Doi Inthanon, Thailand (Bedos 1994). This author sampled soil and leaf litter at five altitudes over several years and recorded

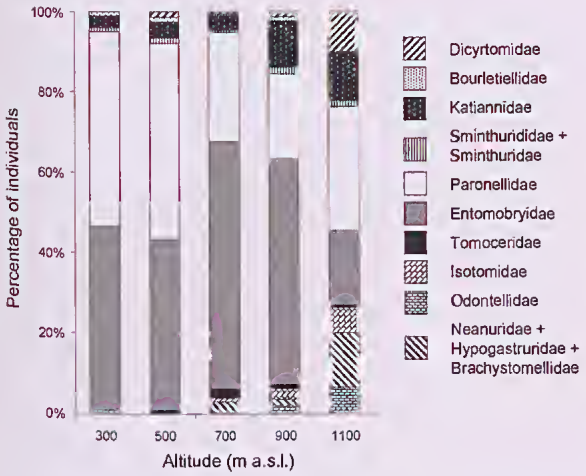


FIG. 1. Proportions of individual of collembolan families collected in pitfall traps at each of the five altitudes (summed across four replicate plots) along the IBISCA-Qld transect.

over 300 species in 106 genera of which only 13 genera also occurred at Lamington. As sampling methods were different, only a small overlap is expected. Most species (140) were collected at middle altitudes (1700–2100 m); the highest altitudes (2400–2550 m), where most samples were taken, had a slightly lower number of species (120) and the lowest altitudes least (109). As sampling was not standardised at all sites some bias in the data may have occurred. Abundance in terms of average individuals per sample was least (89) at intermediate elevations, highest (130) at the highest elevations and intermediate at the lowest elevations (Bedos 1994). Ordination showed some degree of separation with lower elevations (700–1150 m) clustering separately from higher elevations (1700, 2400 and 2550 m).

In a different climatic region on subantarctic Marion Island, species richness and abundance of springtails, collected by funnel extraction, were

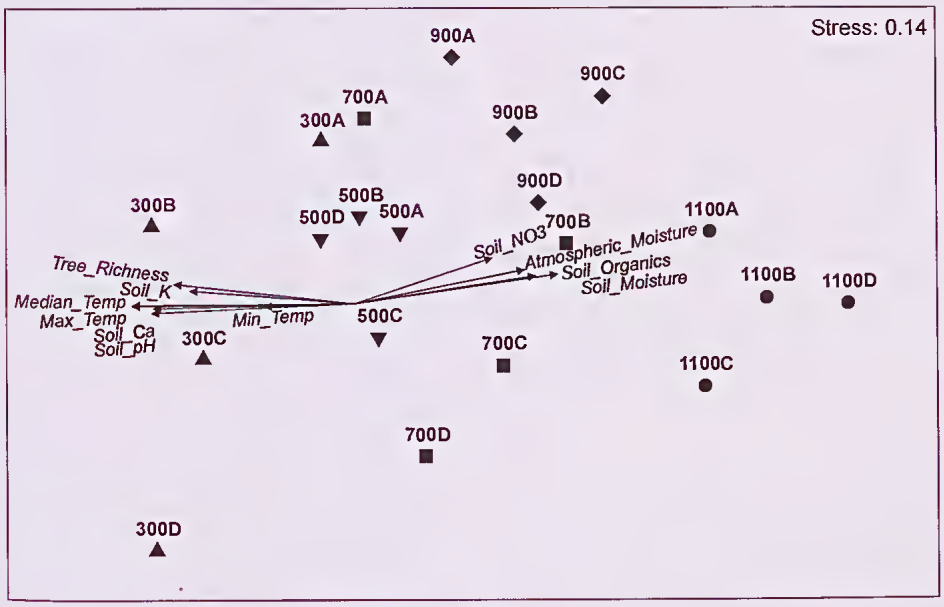


FIG. 2. Non-metric multidimentional scaling (NMDS) ordination plot of collembolan assemblages, based on log transformed abundances of species and morphospecies collected in pitfall traps along the IBISCA-Qld transect in October 2006. Superimposed vectors are environmental parameters significantly correlated ($P<0.05$) to the assemblage composition. ▲, 300 m a.s.l.; ▼ 500 m; ■ 700 m; ◆ 900 m; ●; 1100 m. A, B, C and D correspond to the replicate plots at each altitude.

analysed based on vegetation type (Gabriel *et al.* 2001). Species richness was highest in both the lowland tussock grassland and high altitude fell field sites (9 spp) and lowest in the high altitude mire (5 spp), while mean annual density of all species varied from 305 individuals per m^2 in the mid-altitude fell field to 60733 individuals per m^2 in the *Cotula plumosa* community (Gabriel *et al.* 2001).

In summary there appear to be a few generalisations that can be made concerning changes in diversity and abundance of Collembola with altitude. At most localities, abundance and species richness are lower at the highest altitudes than at mid- or sub-summit altitudes. This agrees with the conclusions of Zapata *et al.* (2003) who tested the null hypothesis that altitudinal or latitudinal gradients exhibit a mid-gradient peak in species richness and concluded that it was not supported. Another common factor is that at Lamington, Tasmania and the Solomon Islands, hemiedaphic and euedaphic families, Isotomidae (and Tullbergiidae in the Solomons), are more abundant at the summit, regardless of actual altitude, while Symphypleona, Entomobryidae and Paronellidae, more epigaeic groups, are in low abundance here or even absent altogether. This is a characteristic that can be demonstrated more widely if one assumes that high altitudes and high latitudes present similar environmental features. For instance, at extremes of latitude, Antarctic faunas lack Symphypleona, Entomobryidae and Paronellidae (Gabriel *et al.* 2001). From this and the Tasmanian data, biotic factors, in particular vegetation structure such as the presence or absence of forest cover, appear to influence the occurrence of families at different localities more than altitude or climate *per se* which exert only an indirect effect through their effects on vegetation. One other possible generalisation is that where species data exist, it appears that a different suite of species, but not genera or families, occurs at the summit of all mountains sampled regardless of location, vegetation and altitude (Greenslade 2008).

The results for Collembola from the Lamington transect that showed only the plots at 1100 m had a distinctly different composition are similar to assemblage patterns of some other invertebrate groups sampled from the same plots. An exception was the ants which showed a linear response to altitude with species richness progressively decreasing and assemblage composition progressively changing with increasing altitude (Burwell & Nakamura 2011). This is probably a response to decreasing temperatures and increasing soil moisture (Strong *et al.* 2011). The data for Coleoptera, some Hemiptera and macrolepidoptera also indicated that the most distinct species assemblages occurred at 1100 m (Ashton *et al.* 2011; Ødegaard & Diserud 2011), although this separation seems most marked for Collembola.

One reason for this may be that ground-living, (that is soil and leaf litter) organisms are less responsive to slight shifts in climatic variables compared with epigaeic species that live predominately above the ground and Collembola are the only ground-living decomposer guild that has been analysed from these studies to date. Collembola may be more strongly influenced by the depth and moisture content of the leaf litter and humus layers than the other invertebrates studied. The pH of the soil becomes more acidic with increasing altitude along the IBISCA-Qld gradient (Laidlaw *et al.* 2011; Strong *et al.* 2011) and Loranger *et al.* (2001) suggested that soil acidity is the primary factor influencing altitudinal distribution of Collembola. It is noteworthy that the vegetation at the highest altitude, 1100 m, is the only site where relictual Gondwanan *Nothofagus* rainforest occurs. We suggest that the main reason for the distinctiveness of the fauna here is that it is largely composed of relictual invertebrate species from Gondwana while lower altitudes tend to harbour more recent and widespread lowland taxa.

A number of species, mainly from the Entomobryidae and Paronellidae, are widespread along the transect. Their value as 'climate

responders' is minimal. However several potential climate responders, that is taxa that appear to have limited altitudinal distributions, were detected in other families, based on the results of a single trapping period and single method (Table 5). First are those, *Rastriopes* sp. and *Spyrotheca* sp., that were found mainly (80%) at the lowest altitudes. *Rastriopes* belonged to the Bourletiellidae, an epigaeic family most abundant and diverse in warm climates and in summer (Greenslade 1991b). It might be expected that under climate change, their altitudinal range would increase. Of most importance are the two species, *Acanthanura* sp. and a species of Pseudachorutinae, only found at 1100 m. In spite of low numbers trapped, we consider that they are truly altitudinally restricted species based on the biology of allied species. Also important is a new species of *Adelphoderia*. This genus is found only where water logging occurs sporadically (Greenslade 1982). It was trapped at a single IBISCA-Qld 500 m plot in close proximity to a creek. Only the 500 m (and some 300 m) sites were close to permanent creeks (there being no other accessible 'drier' sites available at those altitudes). This may well be the explanation for why this species was restricted to the 500 m plot, yet it may well occur at other altitudes close to creek lines. The Odontellidae were not identified to species but about five species were present. It is possible that some might be even more restricted than the family as a whole. They would repay further study. The genus *Triacanthella* has an unusual distribution in Australia being found not only in montane situations as in this study and elsewhere but also sometimes in semiarid mallee or *Melaleuca* and *Casuarina* woodland in coastal situations. It is also found in boreal regions but has not been recorded in the tropics. Finally results for the two genera with sequential distributions, *Cryptopygus* (found at 900-1100 m) and *Isotopenola* (700-900 m) reflect their wider distribution in the Southern Hemisphere. The genus *Cryptopygus* occurs in the Antarctic, subantarctic and southeastern Australia but only in cool, moist localities. On the other hand, *Isotopenola* is not found in the Antarctic or subantarctic but is fairly common in humid parts of south eastern Australia and is found in a wider range of climatic conditions than *Cryptopygus*, indicating that it is tolerant of somewhat warmer conditions. The relative distributions of the species in these two genera clearly suggest they are also candidates as 'climatic responders'.

ACKNOWLEDGEMENTS

Thanks are due to the many volunteers and others who collected and sorted the samples, particularly K. Staunton and D. Putland who conducted the IBISCA-Qld pitfall trapping programme. Thanks also to C. Burwell and A. Nakamura who undertook to the statistical analysis and to referees and editors who greatly improved the manuscript. We are also grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their funding was matched by funding from Griffith University, the Queensland Museum, the Global Canopy Programme, NRM Queensland and the Queensland National Parks Association. We also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reilly's Rainforest Resort. Without all of these sources the project would not have been possible. Sampling activities were covered by a Scientific Purposes permit issued by the Queensland Environmental Protection Agency to Griffith University (permit #WITK03875806).

LITERATURE CITED

Anderson, M.J., Gorley, R.N. & Clarke, K.R. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. (PRIMER-E: Plymouth).

Andrew, N.R., Rodgerson, L. & Dunlop, M. 2003. Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. *Journal of Biogeography* 30: 731–746.

Ashton, A.L., Kitching, R.L., Maunsell, S.C., Putland, D.A. 2011. Investigating macro-lepidopteran assemblages along an altitudinal gradient in subtropical rainforest – exploring indicators of

climate change. *Memoirs of the Queensland Museum-Nature* 55(2): 375-389.

Australian Government, Bureau of Meteorology. 2008. http://www.bom.gov.au/climate/dwo/IDCJDW4057.latest.shtml Accessed October 2008.

Bedos, A. 1994. Les Collemboles édaphiques du massif du Doi Inthanon, Thailande: biodiversité et ecologie en forêt tropicales. Unpubl. Doctoral Thesis, the University of Paul Sabatier, Toulouse, France.

Burwell, C.J. & Nakamura, A. 2011. Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum-Nature* 55(2): 391-411.

Clarke, K.R. & Gorley, R.N. 2006. PRIMER v 6: User Manual/Tutorial. (PRIMER-E: Plymouth).

Dufrêne, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Gabriel, G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A. & Smith, V.R. 2001. Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* 24: 421–430.

Greenslade, Penelope. 1982. Revision of the Spinothecinae (Collembola: Sminthuridae) including a new Australian genus. *Journal of the Australian Entomological Society* 21: 81–95.

Greenslade, Penelope. 1991a. Notes on Australian Uchidanurinae (Collembola: Neanuridae). Pp. 63–65. *In*, G. K. Veeresh, D. Rajagopal, & C. A. Viraktamath (eds) *Advances in Management and Conservation of Soil Fauna*. Proceedings of the 10th Colloquium on Apterygota, Bangalore, India August 1988. (Oxford and IBH Publishing Co. Pvt. Ltd: New Dehli, Bombay and Calcutta).

Greenslade, Penelope. 1991b. Chapter 11 Collembola. Pp. 252–264. *In*, The Insects of Australia. A textbook for students and research workers. 2nd Edition. (Division of Entomology, CSIRO: Australia).

Greenslade, P. 2004. Collembola species identified from the Warra - Mount Weld altitudinal transect. Unpublished Report to Forestry Tasmania, Hobart.

Greenslade, P. 2008. Has survey effort of Australia's islands reflected conservation and biogeographical significance? An assessment using Collembola. *European Journal of Soil Biology* 44(5–6): 458–462.

Greenslade, P. & Sutrisno. 1994. *Epimetrura rostrata* sp. n., *E. mirabilis* Schött, and the status of the genus *Epimetrura* (Collembola: Entomobryidae). *Annales Zoologici Fennici* 195: 52–57.

Grove, S., Doran, N., Driessen, M. & Balmer, J. 2004. Warra – Mount Weld altitudinal transect ecotonal and baseline altitudinal monitoring plots (BAMPs): establishment report (Forestry Tasmania). Technical report no. 17.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA Queensland Project. *Memoirs of the Queensland Museum-Nature* 55(2): 235-250.

Laidlaw, M.J, McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Musenm-Nature* 55(2): 271-290.

Loranger, G., Bandyopadhyaya, I., Razaka, B. & Ponge, J-F. 2001. Does soil acidity explain altitudinal sequences in collembolan communities? *Soil Biology and Biochemistry* 33(3): 381–393.

Leakey, R.J.G. & Proctor, J. 1987. Invertebrates in the litter and soil at a range of altitudes on Gunung Silam, a small ultrabasic mountain in Sabah. *Journal of Tropical Ecology* 3: 119–129.

Maunsell, S.C. 2009. The distribution of leaf-litter springtails (Collembola) in response to environmental changes along a 400m altitudinal gradient in subtropical rainforest. Honours Thesis, School of Environment, Griffith University.

Ødegaard, F. & Diserud, O.H. 2011. Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park (Queensland, Australia). *Memoirs of the Queensland Museum-Nature* 55(2): 395-374.

Rodgers, D. & Kitching, R.K. 1998. Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography* 21: 392–400.

Rodgers, D. & Kitching, R.K. 2010. Rainforest Collembola (Hexapoda: Collembola) and the insularity of epiphyte microhabitats. *Insect Conservation and Diversity* 4: 99–106.

Sattler, P. & Williams, R. (eds.) 1999. The Conservation Status of Queensland's Bioregional Ecosystems. (Environmental Protection Agency: Brisbane).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Putland, D. & Kitching, R.K. 2011. The physical environment

of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Sutrisno 1994. Collembolan Assemblages in Australian Rainforest Canopies. Thesis for Master of Resource Science, Department of Ecosystem Management, University of New England, Armidale, NSW, Australia.

Zapata, F.A., Gaston, K.J. & Chown, S.L. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology* **72**: 677–690.

Thysanoptera of Lamington National Park, Australia, collected during the IBISCA-Queensland Project

Desley J. TREE

Queensland Primary Industries Insect Collection (QDPC), Department of Employment, Economic Development and Innovation, Ecosciences Precinct, GPO Box 267, Brisbane Qld 4001, Australia. Email: desley.tree@deedi.qld.gov.au

Laurence A. MOUND

CSIRO Entomology, PO Box 1700, Canberra ACT 2601, Australia.

Citation: Tree, D.J. & Mound, L.A. 2011 12 20: Thysanoptera of Lamington National Park, Australia, collected during the IBISCA-Queensland Project. *Memoirs of the Queensland Museum – Nature* 55(2): 349-358. Brisbane. ISSN 0079-8835.

ABSTRACT

We documented species of thrips (Thysanoptera) collected during the IBISCA-Queensland Project, an altitudinal study in subtropical rainforest at Lamington National Park, Queensland, Australia. Thrips were identified from samples collected by four methods, leaf litter extracts, Malaise traps, flight interception traps and yellow pan traps, conducted at four plots at each of five altitudinal zones (300, 500, 700, 900 and 1100 metres above sea level) in October 2006 and January and March 2007. A total of 61 thrips species from three families were recorded from these samples. An additional 20 species were recorded from Lamington National Park by targeted collecting for thrips, mostly beating live and dead foliage and branches, bringing the total thrips fauna to 81 species. Biogeographically, the most interesting record was a new species breeding in the flowers of *Pentaceras australis*, *Cranothrips ibisca*, the only eastern species in a western and arid zone genus. ❐ *Thysanoptera, Aeolothripidae, Melanthripidae, Thripidae, Phlaeothripidae, IBISCA-Queensland, altitude.*

The IBISCA-Queensland project was designed to document the current distributions of a range of invertebrate taxa and plants along an altitudinal gradient within continuous rainforest in Lamington National Park, south-east Queensland (see Kitching *et al.* 2011). Twenty permanent study plots were established within the West Canungra Creek catchment of the Green Mountains Section of the park; four replicate plots at each of five zones of elevation (300, 500, 700, 900 and 1100 metres above sea level (a.s.l.)) (see Kitching *et al.* 2011 for precise localities of plots). Between October 2006 and March 2007 baseline sampling of invertebrates was conducted on these plots using a variety of sampling methods. Here we report on species of thrips (Thysanoptera) collected by this baseline sampling as well as additional species collected by targeted hand collecting on the IBISCA-Queensland study plots and elsewhere in the Green Mountains Section of Lamington National Park.

The Thysanoptera, the insect order commonly known as thrips, includes almost 800 described species from Australia (ABRS 2011), out of a world total of about 6000 species (Mound 2011). However, judging from slide-mounted species available in collections at Canberra and Brisbane, it seems likely that an equal number of species remain undescribed from Australia. Estimating the potential size of this fauna is difficult, as thrips populations are commonly

strongly aggregated. As a result, standardised collecting methods based on randomised sampling usually acquire few specimens, although of a considerable diversity of species. However, most thrips species are polymorphic to some extent, and many species are highly polymorphic, such that identification of isolated individuals is not possible. Hand-collecting by specialists is a more effective method of acquiring large samples from strongly aggregated populations, and has the advantage of producing valuable data on host-plant associations and structural variation. But specialist collecting is limited by constraints of time and number of localities sampled. In attempting to contribute to the objectives of IBISCA-Queensland Project (see Kitching *et al.* 2011), we compromised between the above sampling methods. The yield of specimens from within the twenty IBISCA-Queensland study plots was far too low to produce generalisations (Table 1 & 2), and time and space limited the amount of hand collecting that could be achieved. Here we list the thrips species found at Lamington National Park based on our own collecting and available IBISCA-Queensland samples.

METHODS

We examined thrips that had been extracted from samples collected by four of the IBISCA-Queensland baseline sampling methods; Tullgren funnel leaf litter extracts, Malaise traps, flight interception traps (FIT) and yellow pan traps. A single sample from each method was collected from all twenty IBISCA-Qld study plots (4 plots at each elevation, 300, 500, 700, 900 and 1100 m a.s.l.) on three occasions, October 2006, January 2007 and March 2007 (see Kitching *et al.* 2011 for more details). Samples were collected from within a permanent 20 m x 20 m quadrat established in the centre each plot. In total 132 samples containing thrips were examined.

Each litter sample was derived from 1 litre of unsifted leaf litter collected from a single location within the central quadrat of each plot and extracted with a Tullgren funnel for 6 days. Each Malaise trap sample was collected with a Townes type trap operated for 10 days (see Lambkin *et al.* 2011 for more details). Each FIT sample was obtained from a single trap operated for 10 days. Each flight interception trap consisted of a vertical rectangular panel (66 cm x 70 cm) of layers of plastic kitchen wrap above a rectangular collecting container (14 cm x 66 cm) raised above ground level and filled with propylene glycol. Each yellow pan trap sample consisted of three rectangular plastic food containers (approximately 165 mm x 110 mm) placed on ground within the central quadrat and operated for three days. Catches from the three traps pooled into one sample.

In addition to the baseline collecting methods, we conducted targeted collecting for thrips on 9-11 October 2006 and 12-13 March 2007. This mainly involved hand collecting by beating living foliage and flowers, and dead leaves and branches over a white plastic tray. In addition we collected a few thrips from leaf litter and by spraying tree trunks with pyrethroid insecticide. Some of this additional hand collecting was undertaken on the IBISCA-Qld study plots at 900, 700 and 300 m a.s.l., but we also collected in rainforest along walking tracks (Border, Elabana Falls, Wishing Tree and Moran Falls Tracks) mostly between 700 and 950 m a.s.l. We also collected in open areas in the vicinity of O'Reilly's Rainforest Resort and the Green Mountains camping and parking areas.

Adult specimens from nearly all collections were slide-mounted and identified to described species and genera where possible. Specimens have been deposited in the Queensland Primary Industries Insect Collection (QDPC), Brisbane and the Australian National Insect Collection (ANIC), Canberra.

RESULTS

Overall, 211 adult thrips and 45 immature thrips were present in a total of 132 IBISCA-Qld baseline samples examined (16 leaf litter extracts, 31 Malaise, 34 FIT, 51 yellow pan, Table 1). Unfortunately adult thrips were uncommon in samples; only 3 of the 132 samples contained more than 5 adults (the maximum was 8 in a flight interception trap), with many containing only single specimens. Also, nine adult thrips collected from these traps were too damaged to identify, however, the other 202 adult thrips represented 61 species from 3 families. Malaise traps collected the greatest diversity of species and leaf litter showed the least diversity species. Flight interception traps collected the highest numbers of adult thrips with leaf litter extracts yielding the lowest numbers (Table 1). Additional targeted collecting of thrips from IBISCA-Qld plots and elsewhere yielded 41 species, including 20 not collected by the baseline sampling methods. Therefore, combined baseline and targeted collecting methods yielded a total of 81 thrips species from 4 families from Lamington National Park, including 11 species unrecognisable at generic level (Table 2).

The two most common species in the baseline samples were *Thrips setipennis* (total specimens = 35), a common flower feeding species, and *Psalidothrips* sp. (total specimens = 24) a common fungal feeder usually found in leaf litter. However, recently the latter species has been collected by the authors on hanging dead leaves in northern Queensland, and *Psalidothrips* sp. was also captured in flight interception traps.

Larvae were collected by all four baseline sampling methods with most in leaf litter extracts (Table 1) from the lower altitudes of 300 and 500 m a.s.l. The collection of larvae in the Malaise and flight interception traps suggests that they can be carried by wind currents. Very few pupae were found, suggesting they are not carried by the wind and that in leaf litter they may burrow deeper into the soil to pupate. It is usually not possible to identify unassociated larvae and pupae of thrips species.

Biogeographically there were few surprises in the fauna, although the IBISCA-Qld sites seemed to sit on the border between the southern and northern thrips faunas of eastern Australia. The most significant record was a new species of Melanthripidae, *Cranothrips ibisca* Pereyra & Mound, breeding in the flowers of *Pentaceras australis* (Rutaceae). This genus is found mainly in the west and centre of Australia, and this is the first record from the east of the continent.

Individual baseline sampling methods

Leaf litter extracts. Of the 16 leaf litter extracts, 59% contained ≤ 1 adult thrips, 35% between 2 and 5 adults, and 6% more than 5 adults. Nearly all specimens, including larvae were collected at the lower altitudes of 300 and 500 m a.s.l. (Table 2). Only one thrips family was collected in leaf litter, the Phlaeothripidae (Idolothripinae and Phlaeothripinae). One species of Idolothripinae was collected, *Allothrips stannardi*, and this is common in leaf litter in eastern Australia (Mound 1972). Three species of Phlaeothripinae, a group with a diverse range of biologies including feeding on fungal hyphae or plant cells, or predation (Crespi *et al.* 1997; Mound & Morris 2005), were collected in low numbers. Highest numbers of thrips in leaf litter were collected at 300 m a.s.l. in March 2007, and these were mainly *A. stannardi* (Table 2).

Malaise traps. Of the 31 Malaise trap samples examined, 52% contained ≤ 1 adult thrips, 48% between 2 and 5 adults, and none contained more than 5 adults. Representatives of three thrips families were collected; Aeolothripidae, Phlaeothripidae (Phlaeothripinae and Idolothripinae) and Thripidae (Thripinae, Sericothripinae, Panchaetothripinae and Dendrothripinae). Aeolothripids are generally predatory (Mound & Marullo 1998), Thripinae feed on flowers and young leaves (Mound &

TABLE 1. Total number of individuals of different thrips life stages and species (species identified only from adults) collected by four IBISCA-Queensland baseline sampling methods. Data from samples collected across five different altitudinal zones (300, 500, 700, 900 and 1100 m a.s.l.) combined. Numbers in parentheses are those adults that were too damaged to identify.

Collect. method	No. adults	No. species	Phlaeothripidae larvae	Phlaeothripidae pupae	Thripidae larvae	Total samples
Leaf litter	26 (0)	6	18	2	0	16
Malaise	58 (1)	33	5	0	0	31
FIT	65 (4)	21	7	0	0	34
Yellow pan	53 (4)	26	7	0	6	51
Total	202 (9)	61	37	2	6	132

Gillespie 1997), Dendrothripinae feed on young leaves (Mound 1999), and Panchaetothripinae (Mound & Gillespie 1997) generally feed on older leaves. Highest numbers of specimens and species were collected at 900 m a.s.l. and during March 2007, and low numbers at 300 and 1100 m a.s.l. and during October 2006. Malaise trap samples were not dominated by any particular species with all represented by between one and five specimens (Table 2).

Flight interception traps. Of the 34 samples collected by flight interception traps, 56% contained ≤ 1 adult thrips, 38% between 2 and 5 adults, and 6% more than 5 adults. As with Malaise traps, three thrips families were collected; Aeolothripidae, Phlaeothripidae (Phlaeothripinae and Idolothripinae) and Thripidae (Thripinae, Dendrothripinae, and Panchaetothripinae). The highest numbers of specimens and species were collected at 300 m a.s.l. and during October 2006, with lower numbers at 500 and 1100 m a.s.l. and in January 2007. The most common species were *Psalidothrips* sp. (20 specimens), *Thrips setipennis* (17) and *Hoplandrothrips* sp. (6) with all other species represented by one or two specimens (Table 2).

Yellow pan traps. Out of the 51 samples collected by yellow pan traps, 77% contained ≤ 1 adult thrips, 23% between 2 and 5 adults, and none contained more than 5 adults. Only two thrips families were collected, Phlaeothripidae (Phlaeothripinae and Idolothripinae) and Thripidae (Thripinae, Dendrothripinae, and Panchaetothripinae). The numbers of specimens and species were spread fairly evenly over the five altitudes. The most common species were *Thrips setipennis* (14 specimens) and *Parthenothrips dracaenae* (9) with all other species represented by only one or two specimens (Table 2).

DISCUSSION

Within rainforest, a large proportion of thrips species are likely to live on the leaves, flowers and dead branches in the canopy, and for this group of insects the absence of sampling from the tree canopy was particularly unfortunate. Fungus feeding thrips species live on the bark of trees and in leaf litter on the ground, and these were better sampled by the IBISCA-Queensland collecting methods. Understorey shrubs and ferns in the deep shade within rainforest usually support few thrips species, although at Lamington the flowers of *Livistona* palms carried large numbers of the common flower thrips, *Thrips setipennis*. The white flowers of these palms were presumably strongly attractive within the area of low light intensity; large numbers of this flower thrips were similarly noted to land on the white plastic trays that are commonly used for sampling thrips from vegetation. Hand collecting was effective only at breaks in the forest canopy, at tree falls, along the preformed footpaths, and at forest edges. By far the largest number of thrips species was taken

TABLE 2. Checklist of 81 thrips species recorded from the Green Mountains Section of Lamington National Park and the numbers of adult specimens collected from the 20 IBISCA-Queensland study plots stratified by altitude (m a.s.l.), collecting method (LL – leaf litter extract, MT – Malaise Trap, FIT – flight interception trap, YP – yellow pan trap) and sampling time (October 2006, January 2007 and March 2007). Species also recorded by targeted collecting for thrips on the IBISCA-Qld plots and elsewhere in the park, indicated by tick marks.

	Total specimens	Altitude (m a.s.l.)					Sampling methods				Sampling period			Target sampling
		300	500	700	900	1100	LL	MT	FIT	YP	Oct 2006	Jan 2007	Mar 2007	
TEREBRANTIA														
Aeolothripidae														
Andrewarthia kellyana (Bagnall)	2			1	1			1	1		2			✓
Desmothrips bagnalli Karny														✓
Desmothrips tennicornis (Bagnall)	2		1	1				2				1	1	
Erythridothrips cubilis Mound & Marullo														✓
Lamprothrips sp.n.														✓
Melanthripidae														
Cranothrips ibisca Pereyra & Mound														✓
Thripidae														
Dendrothripinae														
Anisopilothrips venustulus (Priesner)	2	2								2			2	
Dendrothrips diaspora Mound	1			1						1	1			
Ensiferothrips primus Bianchi	1		1					1			1			
Ensiferothrips sp. nov.	2				1	1				2	2			✓
Leucothrips nigripennis Reuter	1		1							1			1	
Panchaetothripinae														
Bhattithrips frontalis (Bagnall)	2	1		1				1	1			1	1	
Caliothrips striatopterus (Kobus)	1				1					1	1			
Hercinothrips femoralis (Reuter)	2	1	1							2			2	
Heliothrips haemorroidalis (Bouché)	5	2		2	1			2	1	2	1		4	✓
Parthenothrips dracaenae (Heeger)	10	3	1	4		2		1		9	4		6	
Phibalothrips longiceps (Karny)	1	1						1				1		
Sericothripinae														
Hydatothrips williamsi Mound & Tree	1				1			1					1	

TABEL 2. cont...

	Total specimens	Altitude (m a.s.l.)					Sampling methods				Sampling period			Target sampling
		300	500	700	900	1100	LL	MT	FIT	YP	Oct 2006	Jan 2007	Mar 2007	
Thripinae														
Anaphothrips sp.														✓
Chaetanaphothrips sp.														✓
Frankliniella occidentalis (Pergande)	1					1				1	1			
Frankliniella schultzei (Trybom)	1				1			1				1		
Mycterothrips desleyae Masumoto & Okajima														✓
Pezothrips kellyanus (Bagnall)	1	1								1	1			✓
Pseudanaphothrips pallidus (Steele)	1			1						1	1			✓
Pseudanaphothrips sp.	1			1					1				1	✓
Scirtothrips albomaculatus Bianchi														✓
Thrips australis (Bagnall)	1			1						1	1			✓
Thrips coloratus Schmutz	1				1				1				1	
Thrips imaginis Bagnall	2		1			1		1		1	1		1	✓
Thrips setipennis (Bagnall)	35		4	7	7	17		4	17	14	31	2	2	✓
Thrips tabaci														✓
Trichromothrips sp. nov.	1				1			1				1		✓
TUBULIFERA														
Phlaeothripidae														
Idolothripinae														
Acallurothrips sp.														✓
Allothrips staunardi Mound	10	10					10					2	8	✓
Bactrothrips sp.														✓
Carieutothrips sp. nov.														✓
Carientothrips mjobergi ag.	2			1	1			1	1		1		1	✓
Ecacleistothrips glorious Mound	1	1						1				1		
Ethirothrips sp.	1				1			1					1	✓
Idolothrips dissimilis Girault	1			1						1			1	✓

TABEL 2. cont...

	Total specimens	Altitude (m a.s.l.)					Sampling methods				Sampling period			Target sampling
		300	500	700	900	1100	LL	MT	FIT	YP	Oct 2006	Jan 2007	Mar 2007	
Idolothrips spectrum Haliday														✓
Nesothrips propinquus (Bagnall)														✓
Phaulothrips sp. nov.	2			1	1			2					2	
Gen. nr. *Celidothrips*	1			1						1			1	
Gen. nr. *Ethirothrips*	2		1		1			2			1		1	
Gen. nr. *Polytrichothrips*	1		1					1				1		
Phlaeothripinae														
Baenothrips moundi (Stannard)	2		2					1		1	1		1	
Deplorothrips sp.	2				2				2				2	
Enoplothrips bagnalli Hood														✓
Gen. nr. *Gynaikothrips*	5	2		2	1			5				5		
Haplothrips anceps Hood	1				1					1	1			
Haplothrips bituberculatus (Girault)	1			1			1				1			✓
Haplothrips froggatti Hood	1				1			1			1			✓
Haplothrips victoriensis Bagnall														✓
Haplothrips sp.	6	3			2	1		4	2		1	5		✓
Holothrips sp.														✓
Gen. nr. *Hoplandrothrips*					1					1	1			
Hoplandrothrips sp.	8	2		3	3			2	6		2	3	3	
Hoplandrothrips xanthocnemis (Karny)														✓
Hoplothrips melanurus (Bagnall)														✓
Hoplothrips sp.	2	1				1		1	1			1	1	
Horistothrips australiae Morgan	2			2					1	1	1		1	
Katothrips tityrus (Girault)	1	1						1			1			
Leeuwenia diospyri Mound	1			1				1				1		✓
Leeuwenia polyosmae Mound	1					1		1					1	✓
Liothrips sp.	1	1						1				1		✓
Lissothrips sp.	1				1					1			1	

TABEL 2. cont...

	Total specimens	Altitude (m a.s.l.)				Sampling methods				Sampling period		Target sampling
		300	500	700	900	1100	LL	MT	FIT	YP	Oct 2006	Jan 2007	Mar 2007	
Litiletothrips sp.	5				2	3		2	1	2		1	4	
Psalidothrips taylori Mound & Walker	2	2							2				2	
Psalidothrips sp.	24	12	3	6	3			3	20	1	5	8	11	✓
Stigmothrips/Adraneothrips	4	1	3				4				1		3	
Teuchothrips sp.	7	2	2			3		5	2			2	5	✓
Xylaphothrips sp.	3	2	1				1			2	1		2	
Zeniathrips biseta Mound	3	3					3					3		
Gen. nov. Phlaeo "F"	8	2	6				7		1		4	1	3	
Gen. nov. Phlaeo "H"	1			1					1		1			
Gen. nov. Phlaeo "J"	2			1	1				1	1			2	
Gen. nov. Phlaeo "K"	1				1			1			1			
Gen. nov. Phlaeo "L"	2	2							1	1			2	
Gen. nov. Phlaeo "M"	5		1	2	2			4	1		2	2	1	
Total species	61	23	16	23	26	10	6	33	21	26	31	21	36	41
Total adults	202	58	30	43	40	31	26	58	65	53	75	44	83	

on trees, shrubs and herbs around the car park at O'Reilly's Rainforest Resort at approximately 900 m a.s.l. *Haplothrips victoriensis* was found in particular abundance around this site, on a range of plants. This species is typical of southern Australia (Mound & Minaei 2007), with a natural distribution scarcely extending into Queensland. High populations at the O'Reilly's Rainforest Resort car park probably result from southerly winds transporting this and other thrips species, and depositing them on the ridge of the Lamington forests. Such winds are also considered likely to explain the presence of a recently described species of *Cranothrips* from the same site (Pereyra & Mound 2009).

Almost all of the species in the suborder Terebrantia listed in Table 2 were found at forest edges by hand collecting. These are flower- and leaf-living species, and all are common at ground-level. In contrast, among the Aeolothripidae, *Erythridothrips* and *Lamprothrips* species are rarely collected and are thought likely to live in the canopy. Among the Tubulifera, the species of the subfamily Idolothripinae are assumed all to feed by ingesting fungal spores (Mound & Palmer 1983; Mound 2007) and the listed species were taken within the forest from dead branches, hanging dead leaves, or from tree trunks. Of the subfamily Phlaeothripinae, about half of the listed species are fungus-feeding, presumably on fungal hyphae (Mound 2007) and these similarly live particularly in leaf-litter but also on dead branches and tree trunks. The remaining Phlaeothripinae are known to be associated with living plant tissues.

Three of the *Haplothrips* species are certainly not associated with forests, although *H. bituberculatus* is apparently a predatory species that lives on dead branches and is sometimes taken within forests (Mound & Minaei 2007). The recorded species of *Leeuwenia* (Mound 2004) and *Liothrips* (Mound & Morris 2005) are gall-inducing, host-specific species, and this is probably also true of the *Gynaikothrips* and *Litotetothrips* species for which no host has yet been established. *Euoplothrips bagnalli* is a kleptoparasite within the galls of other thrips in rainforest (Marullo 2001; Mound & Morris 2005) and was found within *Liothrips* galls on *Piper novae-hollandiae*.

ACKNOWLEDGEMENTS

We thank Roger Kitching (Project leader), David Putland, and Heather Christensen for organising our participation in the IBISCA-Queensland Project. As such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the Federal department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. This work would not have been possible without the assistance of numerous volunteers and we thank all IBISCA-Queensland participants for their collaboration.

LITERATURE CITED

ABRS 2011. http://www.environment.gov.au/biodiversity/abrs/

Crespi, B.J., Carmean, D.A. & Chapman, T.W. 1997. Ecology and evolution of galling thrips and their allies. *Annual Review of Entomology* **42**: 51-71.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum – Nature* **55**(2): 235-250.

Lambkin, C.L., Boulter, S.L., Starick, N.T., Cantrell, B.K., Bickel, D.J., Wright, S.G., Power, N., Schutze, M.K., Turco, F., Nakamura, A. & Burwell, C.J. 2011. Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an Australian subtropical rainforest: one hundred thousand and counting. *Memoirs of the Queensland Museum – Nature* **55**(2): 315-331.

Marullo, R. 2001. Gall thrips of the Austro-Pacific genus *Euoplothrips* Hood (Thysanoptera), with a new species from Australia. *Journal of Insect Systematics and Evolution* **32**: 93-98.

Mound, L.A. 1972. Polytypic species of spore-feeding Thysanoptera in the genus *Allothrips* Hood (Phlaeothripidae). *Journal of the Australian Entomological Society* **11**: 23-36.

Mound, L.A. 1999. Saltatorial leaf-feeding Thysanoptera (Thripidae: Dendrothripinae) from Australia and New Caledonia with newly recorded pests of ferns, figs and mulberries. *Australian Journal of Entomology*. **38**: 257-273.

Mound, L.A. 2004. Australian long-tailed gall thrips (Thysanoptera: Phlaeothripinae, Leeuweniini), with comments on related Old World taxa. *Australian Journal of Entomology*. **43**: 28-37.

2007. New Australian spore-feeding Thysanoptera (Phlaeothripidae: Idolothripinae). *Zootaxa* **1604**: 53-68.

2011. *Thysanoptera (Thrips) of the World – a checklist*. http://www.ento.csiro.au/thysanoptera/worldthrips.html

Mound, L.A. & Gillespie, P.S. 1997. *Identification Guide to Thrips Associated with Crops in Australia*. (NSW Agriculture: Orange).

Mound, L.A. & Marullo, R. 1998. Biology and identification of Aeolothripidae (Thysanoptera) in Australia. *Invertebrate Taxonomy* **12**: 929-950.

Mound, L.A. & Minaei, K. 2007. Australian insects of the *Haplothrips* lineage (Thysanoptera – Phlaeothripinae). *Journal of Natural History* **41**: 2919-2978.

Mound, L.A. & Morris, D.C. 2005. Gall-inducing Thrips: An Evolutionary Perspective. Pp. 59-72. *In*, Raman, A. Schaefer, C.W. & Withers, T.M. (eds) *Biology, Ecology, and Evolution of Gall-inducing Arthropods*. (Science Publishers, Inc.: Enfield, USA).

Mound, L.A. & Palmer, J.M. 1983. The generic and tribal classification of spore-feeding Thysanoptera

(Phlaeothripidae: Idolothripinae). *Bulletin of the British Museum (Natural History). Entomology.* 46: 1-174.

Pereya, V. & Mound, L.A. 2009. Phylogenetic relationships within the genus *Cranothrips* (Thysanoptera, Melanthripidae) with consideration of host associations and disjunct distributions within the family. *Systematic Entomology* 34: 151-161.

Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park (Queensland, Australia)

Frode ØDEGAARD

Ola H. DISERUD

Norwegian Institute for Nature Research (NINA), PB 5685 Sluppen, NO-7485 Trondheim, Norway.
Email: frode.odegaard@nina.no

Citation: Ødegaard, F. & Diserud, O.H. 2011 12 20: Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park (Queensland, Australia). *Memoirs of the Queensland Museum—Nature* 55(2): 359-374. Brisbane. ISSN 0079-8835.

ABSTRACT

This study describes the taxonomic composition of Coleoptera and selected groups of Hemiptera (Heteroptera and Coleorrhyncha) and Hymenoptera (Mutillidae) in the understorey of a subtropical rainforest along an altitudinal gradient in Lamington National Park, Queensland, Australia. The altitudinal gradient was subdivided into five zones (300, 500, 700, 900 and 1100 m above sea level (a.s.l.)) within each of which, four replicated sampling sites were established. A total of 16 783 individuals from 1219 species of Coleoptera, 715 from 92 species of Hemiptera and 105 from 17 species of Mutillidae were collected from beating low vegetation. Total species richness and abundance were generally high throughout the gradient, with more than 3000 individuals from over 400 species at each of the five altitudinal zones, but significantly fewer species and individuals were present at higher elevations (900 and 1100 m a.s.l.). Different taxonomic groups showed various patterns of altitudinal zonation, with many groups restricted to the higher elevations, particularly at 1100 m. Of the species unique to one altitudinal zone, half were restricted to 1100 m. The results of the present study provide important base-line data upon which predictions can be made in early warning monitoring systems with regard to climatic change. ❐ *IBISCA, Hemiptera, Hymenoptera.*

The insect fauna of Australian rainforests is highly diverse with a large proportion of endemic taxa (Naumann 2000; Austin *et al.* 2004). There is a number of studies on the community structures of insects in these forests (e.g. Basset 1991; Kitching & Arthur 1993; Grove 2002; Stork & Grimbacher 2006, Wilson *et al.* 2007a). However, these studies are often restricted to certain taxonomic groups the fauna of particular tree species, habitats or strata (Kitching *et al.* 2001). Large data sets of insect assemblages from different tropical forests are key components to understand ecosystem patterns and processes (Huston & Gielbert 1996; Basset 2001). Differences or change in such assemblages may have implications for ecosystem functioning and conservation issues (e.g. Didham 1997; Watt *et al.* 1997; Basset *et al.* 2003; Stork *et al.* 2007; Chen *et al.* 2009).

Assemblage structure and diversity of insect communities change substantially along altitudinal gradients (Hågvar 1976; Janzen *et al.* 1976; Stork & Brendell 1990; Stevens 1992; Olson

1994; Andrew *et al.* 2003; Brehm & Fiedler 2003; Wilson *et al.* 2007a; Colwell *et al.* 2008). In general, species diversity decreases with altitude (Stevens 1992), however, a peak of diversity is often seen at mid elevations (Janzen *et al.* 1976; Olson 1994, Wilson *et al.* 2007b; Colwell *et al.* 2008). In addition, diversity does not change consistently across taxonomic groups (Stork & Brendell 1990). Low species richness at higher elevations may reflect the lower rates of invasion and higher rates of extinction of populations that colonise them, as well as differences in abiotic factors (MacArthur 1972; Stevens 1992).

The target taxa of this study include diverse and ecologically important components of the arthropod fauna. The beetles are the most species rich and ecologically diverse order of insects (Lawrence *et al.* 2000) with an estimated 100 000 species in Australia (Yeates *et al.* 2003). However, knowledge of beetles is very poor in this continent with, approximately, only 28 300 species currently described (Lawrence & Britton 1994). The Heteroptera include about 2100 described Australian species, which is about half of the estimated Australian fauna (Cassis & Gross 1995, 2002). The velvet ants (Mutillidae) are wasps that are parasitic on other wasps, bees or ants, and they include several hundred largely unstudied and undescribed Australian species (Austin *et al.* 2004).

The aims of the present study was to describe the taxonomic composition of selected insect groups in the lower strata of a subtropical rainforest, and to build up knowledge on how insect communities change along altitudinal gradients. In order to predict the effects of future climatic changes, it is essential to accumulate such baseline knowledge upon which predictions can be made. One of the predicted scenarios of climate change is a faunal shift to higher elevations due to elevated temperatures and reduced precipitation (Stork *et al.* 2007), which may result in lowland biotic attrition and mountaintop extinctions (Wilson *et al.* 2007b; Colwell *et al.* 2008; Chen *et al.* 2009). As tropical mountaintop biotas of the tropics, to a large extent, consist of endemic taxa, (e.g. Bell *et al.* 2002) such scenarios of climate change may cause severe species extinctions. In this case, it is particularly important to identify taxonomic components susceptible to such changes in order to develop early warning monitoring systems (Moritz *et al.* 2001).

MATERIAL AND METHODS

Study area. This study was carried out along an altitudinal transect in Lamington National Park, Queensland, Australia. Rainforests within this park can be classified into several structural types including warm subtropical, cool subtropical, warm temperate and cool temperate rainforests (Williams *et al.* 1984; Laidlaw *et al.* 2011). Rainfall averages 1830 mm with most falling during the summer months and at higher elevations (see also Strong *et al.* 2011). Insect samples were obtained from four plots at each of five different elevations; 300, 500, 700, 900, and 1100 m above sea level (a.s.l.). 'Lower elevations' and 'higher elevations' were defined as 300 to 700 m a.s.l., and 900 to 1100 m a.s.l., respectively. Locations and elevations of the individual plots are given by Kitching *et al.* (2011).

Collecting method. Insects were sampled by beating vegetation, using a 1.5 m long beating stick and a 1 x 1 m nylon sheet for collecting the falling material. Vegetation included all structures, foliage and the trunks of large trees to thin branches, both living and dead. Each sample was obtained by beating all reachable vegetation on both sides of a 20 m long transect starting just outside the 20 x 20 m standard IBISCA plots (see Kitching *et al.* 2011) and walking in a straight line away from the plot. A forest area of approximately 3 x 20 m (60 m^2), and a forest volume of 60 m^2 x 3 m height (180 m^3) was covered by each sample. A total of 10 parallel samples (10 transects) were taken at each plot, all performed in different directions from the same starting point to prevent

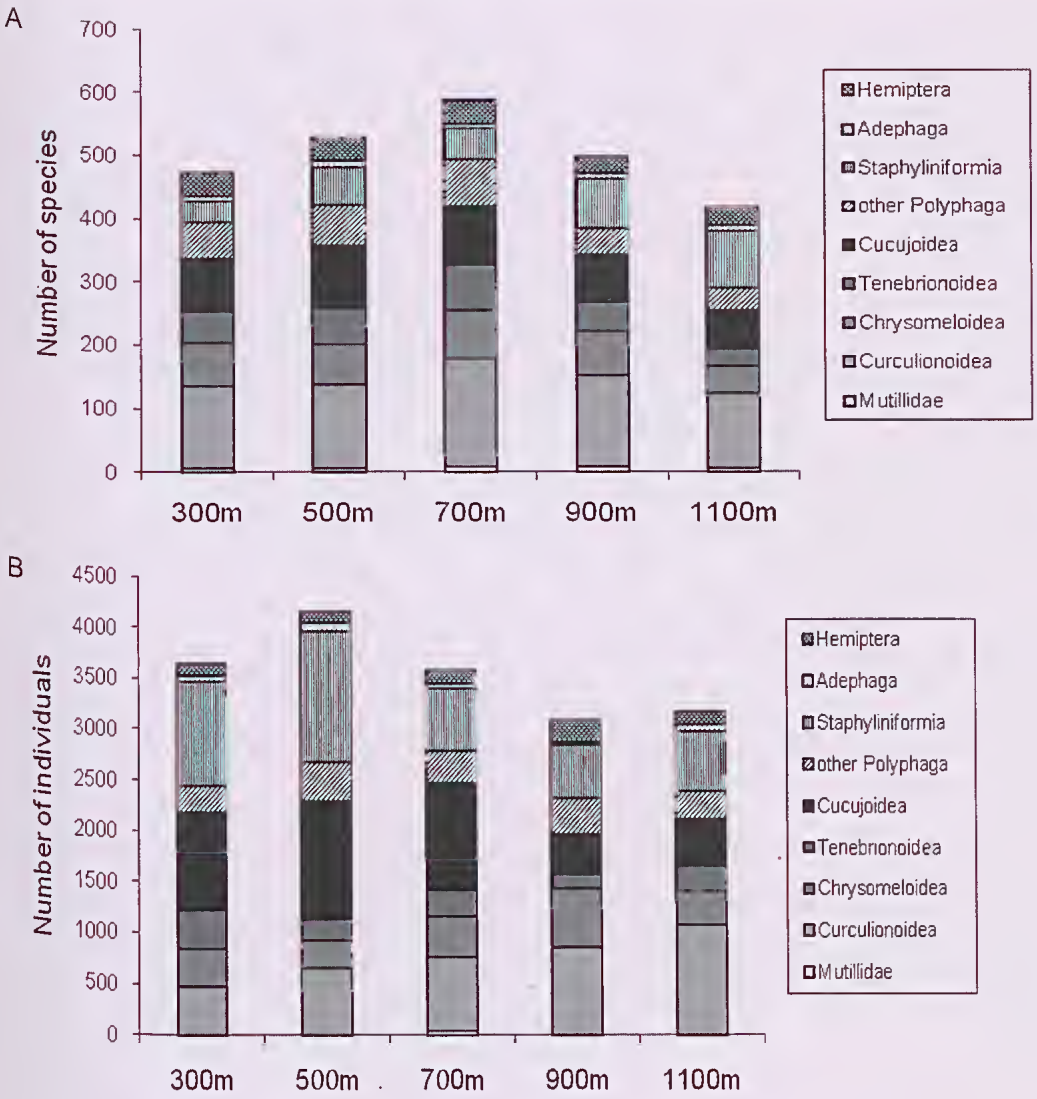


FIG. 1. Total species richness; A, and abundances; B, of different taxonomic groups at the five altitudinal zones. The composite group 'other Polyphaga' includes the Scarabaeiformia, Elateriformia, Bostrichiformia and Cleroidea within the Cucujiformia.

re-beating of the same area. Catches from the 10 parallel samples in each plot were pooled before analyses. The sampling procedure was replicated at three different periods of the year, each representing a different season: spring (6 to 24 October 2006), autumn (8 to 28 March 2007) and summer (14 to 30 January 2008). Accordingly, a total of 600 samples was obtained (10 samples x 20 plots x 3 seasons).

Material. Each sample of beaten material was collected in a zip-lock bag and all samples were sorted into different target groups the same day. The target taxonomic groups, which consist

of a wide range of feeding guilds, included beetles (Coleoptera), true bugs (Heteroptera including Coleorrhyncha) and velvet ants (Mutillidae, Hymenoptera). All specimens of these groups were dry mounted, labelled, sorted into morphospecies and databased. The collection is stored in the first author's collection at the Norwegian Institute for Nature Research (NINA).

Statistical analyses. The data were first collated into nine taxonomic groups (Hemiptera, Adephaga, Staphyliformia, 'other Polyphaga', Cucujoidea, Tenebrionoidea, Chrysomeloidea, Curculionoidea, Mutillidae). Individual groups were analysed separately for species richness and abundance. The groups were treated as independent of each other, so testing the effect of altitude on their responses has been performed on each group separately. The variation between plots of the same altitude and the seasonal variation were not incorporated in these analyses, but may introduce a systematic bias in the estimated variance within the altitudes. In these analyses we considered altitude to be a categorical variable with five levels, so the test was a standard one-way ANOVA. We also performed post-hoc two-sample equal variance *t*-tests between pairs of adjacent altitudinal zones and low (300, 500 and 700 m) versus high (900 and 1100 m) elevational groups. All statistical analyses were performed with the free statistical software R (R Development Core Team 2008).

RESULTS

The material gave a total of 16783 Coleoptera individuals sorted to 1219 species of 70 families. The Hemiptera material consisted of 715 specimens sorted to 92 species of 13 families of the suborder Heteroptera and one family of Coleorrhyncha (Peloridiidae). Hymenoptera material consisted of 105 velvet ants (Mutillidae) belonging to 17 species. The number of species and abundance of each family collected at each elevation are presented in Appendix 1.

The altitudinal distribution of total species richness showed a peak at 700 m (Fig. 1a), a pattern that seems to be driven by many taxonomic groups including Cucujoidea, Tenebrionoidea, Chrysomeloidea and Mutillidae (Fig. 2). There was significantly lower species richness at higher elevations (Fig. 1, see also Tables 1, 2). This pattern was reflected in the species richness of most taxonomic groups including the Cucujoidea, Tenebrionoidea and other Polyphaga, with the exception of Staphyliniformia whose species richness increased at higher elevations (Fig. 2, Table 2).

The number of individuals was largest at 500 m with significantly less individuals at higher elevations (900 and 1100 m) (Fig. 1, see also Tables 1, 2). These patterns were driven by differences in several taxonomic groups including Staphyliniformia, Cucujoidea and the Tenebrionoidea whose abundance decreased at higher elevations (Fig. 3). The abundance of Curculionoidea increased gradually all along the elevation gradient, and species richness was significantly greater at the higher compared to the lower altitudinal group (Table 2).

Particular families showed very pronounced patterns of altitudinal zonation. The large number of weevils at higher elevations (Fig 3) were mainly caused by the wood-boring subfamiliy Cryptorhynchinae (see Appendix 1). The beetle families Byrrhidae and Phloeostichidae, and the bug families Peloridiidae, Enicocephalidae and Schizopteridae were almost exclusively found at 1100 m, while no families were restricted to the lower elevations. High abundance and species richness of Staphyliniformia and Lygaeidae were also found at higher altitudes (Appendix 1). The Adephaga (Carabidae in this case) were also significantly more abundant and species rich at 1100 m compared to 900 m (Table 2).

A total of 185 species (14%) were exclusively found at 1100 m, and when we also include species restricted to 900 m (105 spp) and both 900 m and 1100 m (61 spp), a total

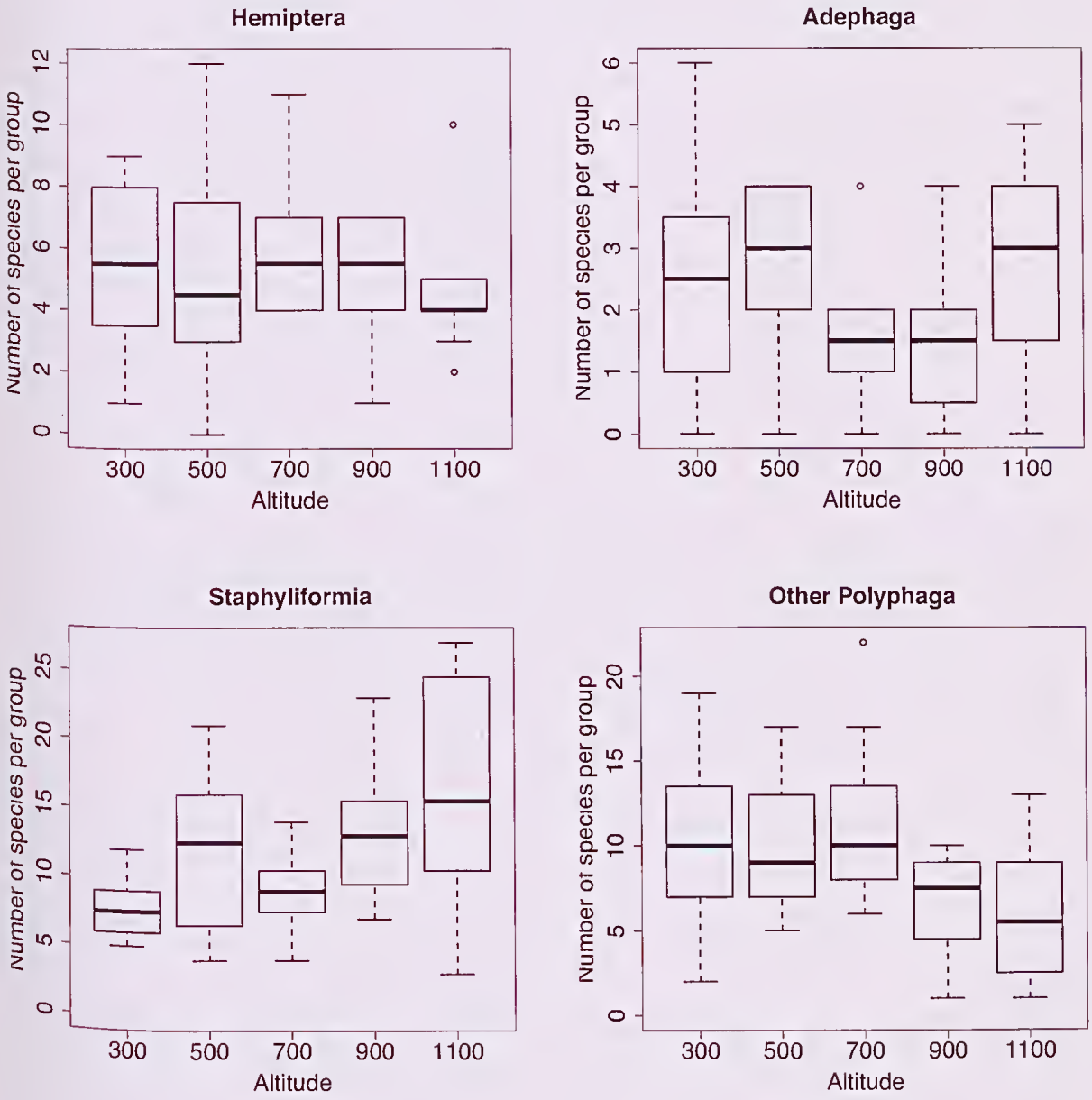
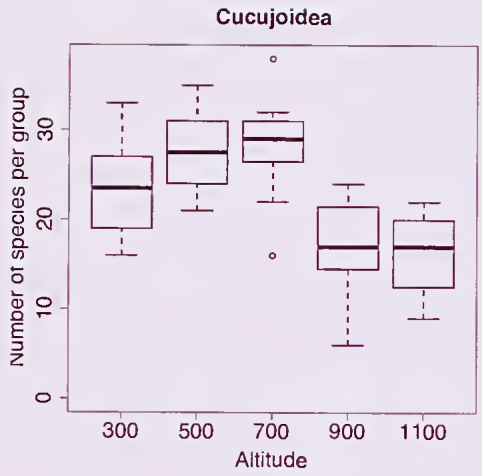
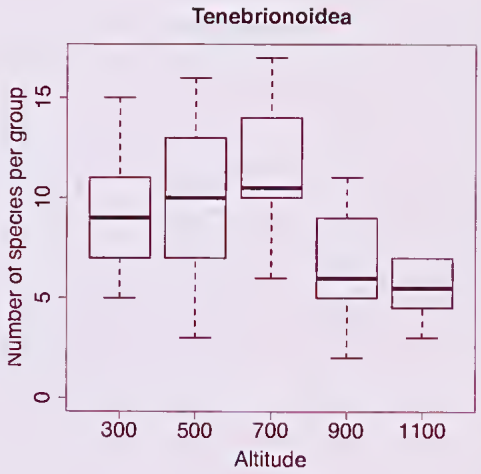
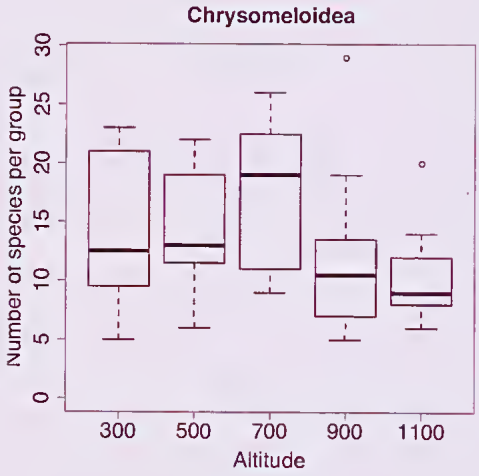
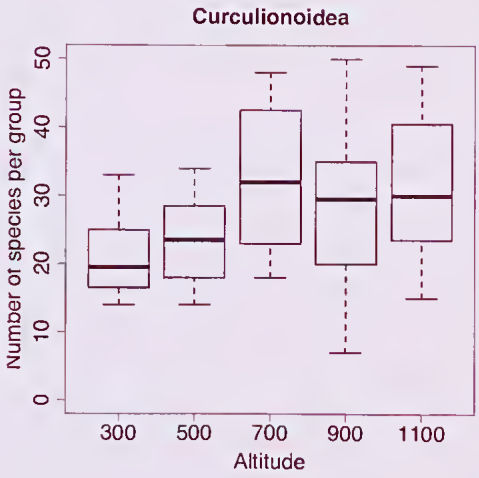


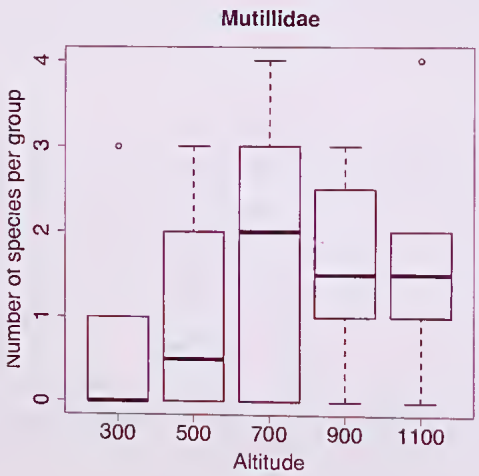
FIG. 2. (This page and opposite) Box-plots for species richness of the nine taxonomic groups and all groups combined ('total') at five different altitudinal zones. The composite group 'other Polyphaga' includes the Scarabaeiformia, Elateriformia, Bostrichiformia and Cleroidea within the Cucujiformia.


Cucujoidea
Number of species per group
0
10
20
30
300
500
700
900
1100
Altitude


Tenebrionoidea
Number of species per group
0
5
10
15
300
500
700
900
1100
Altitude


Chrysomeloidea
Number of species per group
0
5
10
15
20
25
30
300
500
700
900
1100
Altitude


Curculionoidea
Number of species per group
0
10
20
30
40
50
300
500
700
900
1100
Altitude


Mutillidae
Number of species per group
0
1
2
3
4
300
500
700
900
1100
Altitude

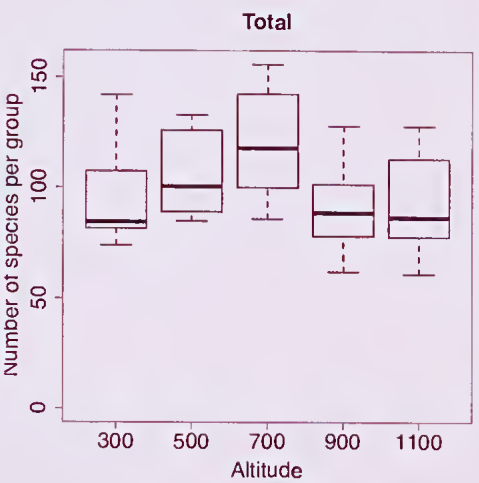

Total
Number of species per group
0
50
100
150
300
500
700
900
1100
Altitude

TABLE 1. *P*-values from one-way ANOVA tests for differences in the number of individuals and species richness of the nine taxonomic groups and all groups combined ('total') among the five altitudinal zones. The composite group 'other Polyphaga' includes the Scarabaeiformia, Elateriformia, Bostrichiformia and Cleroidea within the Cucujiformia.

Group	individuals	species
Hemiptera	0.2451	0.7579
Adephaga	0.0912	0.0392*
Staphyliformia	0.0000 ***	0.0009 ***
Other Polyphaga	0.6258	0.0057 **
Cucujoidea	0.0000 ***	0.0000 ***
Tenebrionoidea	0.0001 ***	0.0000 ***
Chrysomeloidea	0.0228 *	0.0320 *
Curculionoidea	0.0058 **	0.0142 *
Mutilidae	0.05407	0.0682
Total	0.0488*	0.0121 *

TABLE 2. Significant *P*-values ($p<0.05$) representing differences in species richness (spp.) and abundance (ind.) between pairs of different altitudinal zones, or groups of altitudinal zones for nine taxonomic groups and all groups combined. Altitudinal zones of 300, 500 and 700 m were grouped as lower elevation (low el.), and 900 and 1100 m grouped as higher elevation (high el.). The composite group 'other Polyphaga' includes the Scarabaeiformia, Elateriformia, Bostrichiformia and Cleroidea within the Cucujiformia.

	300 m vs. 500 m		500 m vs. 700 m		700 m vs. 900 m		900 m vs. 1100 m		low el. vs. high el.	
	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.
Hemiptera	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Adephaga	n.s.	n.s.	n.s.	0.0108	n.s.	n.s.	0.0385	0.0233	n.s.	n.s.
Staphyliniformia	n.s.	0.0298	0.0001	n.s.	n.s.	n.s.	n.s.	n.s.	0.0004	0.0003
other Polyphaga	n.s.	n.s.	n.s.	n.s.	n.s.	0.0087	n.s.	n.s.	n.s.	0.0002
Cucujoidea	n.s.	0.0482	n.s.	n.s.	<0.0001	0.0001	n.s.	n.s.	<0.0001	<0.0001
Tenebrionoidea	0.0012	n.s.	n.s.	n.s.	0.0124	0.0007	0.0434	n.s.	0.0189	<0.0001
Chrysomeloidea	n.s.	n.s.	0.0459	n.s.	n.s.	0.0374	0.0453	n.s.	n.s.	0.0041
Curculionoidea	n.s.	n.s.	n.s.	0.0185	n.s.	n.s.	n.s.	n.s.	0.0018	n.s.
Mutillidae	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
All groups	n.s.	n.s.	n.s.	n.s.	n.s.	0.0062	n.s.	n.s.	0.0085	0.0255

of 351 species (26.4%) were restricted to higher elevations. However, as rare species may be found at one particular elevation by chance, we repeated the calculations for species with more than 5 individuals in the total samples. The pattern remained the same with as many as 86 (16.5%) out of 522 species restricted to higher elevations (900 and 1100 m). Of the 72 species (with more than 5 individuals) unique to one elevation, half (50 %) were restricted to 1100 m (Fig. 4).

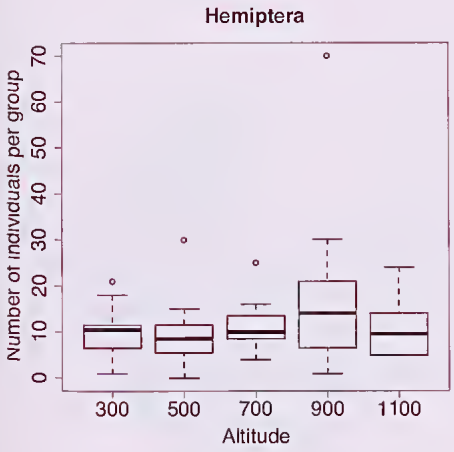
DISCUSSION

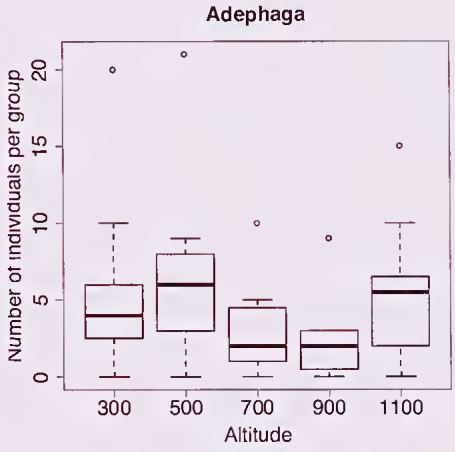
The present study found decreasing abundance and species richness of insects at higher elevations which agrees with most studies of species diversity along altitudinal gradients (Stork & Brendell 1990; Stevens 1992). However, the span of elevations in the present study was probably not large enough to see the prominent diversity declines such as those normally seen at even higher elevations, e.g. between 1500 and 3500 m a.s.l. (Brehm & Fiedler 2003; Wilson *et al.* 2007b; Chen *et al.* 2009). Decrease in diversity with altitude may be explained by parameters such as climatic factors and metapopulation structures (Hågvar 1976; Janzen *et al.* 1976; Stork & Brendell 1990; Stevens 1992; Olson 1994; Andrew *et al.* 2003; Brehm & Fiedler 2003). In addition, the vegetation structure at the 1100 m plots differs from the others by having a significantly smaller number of tree species and a much more prominent epiphyte flora. However, the total effects of these contrasting factors on species diversity are unknown, and investigation of individual parameters is beyond the scope of the present paper.

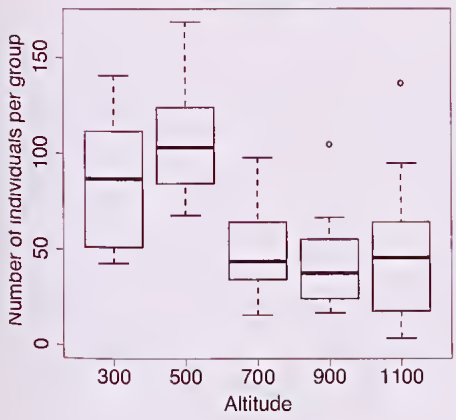
Community structure of insects may be measured at larger taxonomic scales. For instance, if the distributions of specific resources change along altitudinal gradients, relative abundances of particular feeding guilds may be used to capture differences in community structure of insects. However, larger taxonomic scales may mask changes in species composition nested within the same taxonomic group or feeding guild (Grimbacher & Stork 2007). In order to detect such changes, it is necessary to scale down the taxonomic resolution of the target groups as much as possible, ideally to the species level. For instance, overall abundance of Staphyliniformia decreased with increased altitude. Only species-level identification revealed the intriguing pattern that some extremely common species predominate at lower altitudes, while the higher elevations are characterised by a unique and species rich fauna. On the other hand, if species assemblages respond similarly to environmental factors, responses may be readily detectable for nested taxonomic groups or feeding guilds. Hence, the identification of proper target taxa or guilds for early warning monitoring systems is a key stone in order to detect changes, such as climate warming.

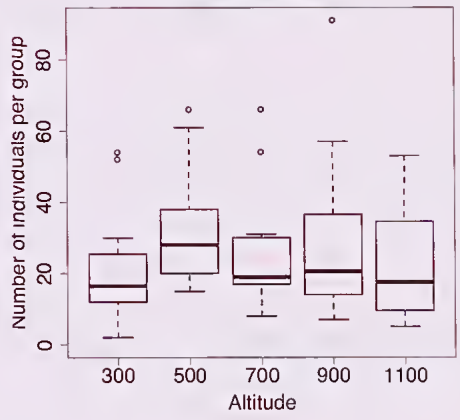
The present study is based on samples from only one forest stratum (understorey) and particular tree species where processes may not be representative of other strata or tree species. Tree species may be affected differentially by climatic changes and elevated CO_2 levels due to their unique characteristics such as different root structures, hydraulic properties or photosynthetic rates (Stork *et al.* 2007). The effects of climate change may be more pronounced in canopy than the understorey, for example, through changes in leaf traits. However, the structures of feeding guilds of beetles in the canopy of tropical rainforests in northern Australia did not differ from that at ground level (Grimbacher & Stork 2007).

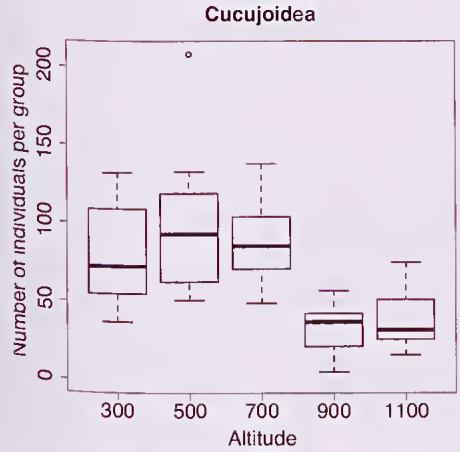
A large proportion of the species in this study were restricted to higher elevations. Due to the large proportion of rare species, however, the exact proportion of high-altitude specialists remains unknown. In the case of this study, the true percentage of species restricted to higher elevations should probably lie somewhere be-

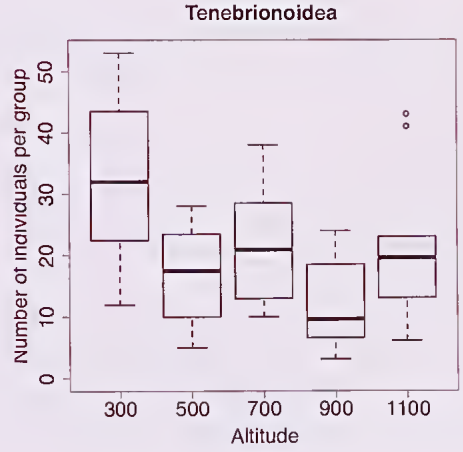

Hemiptera
Number of individuals per group
0
10
20
30
40
50
60
70
300
500
700
900
1100
Altitude


Adephaga
Number of individuals per group
0
5
10
15
20
300
500
700
900
1100
Altitude


Staphyliformia
Number of individuals per group
0
50
100
150
300
500
700
900
1100
Altitude


Other Polyphaga
Number of individuals per group
0
20
40
60
80
300
500
700
900
1100
Altitude


Cucujoidea
Number of individuals per group
0
50
100
150
200
300
500
700
900
1100
Altitude


Tenebrionoidea
Number of individuals per group
0
10
20
30
40
50
300
500
700
900
1100
Altitude

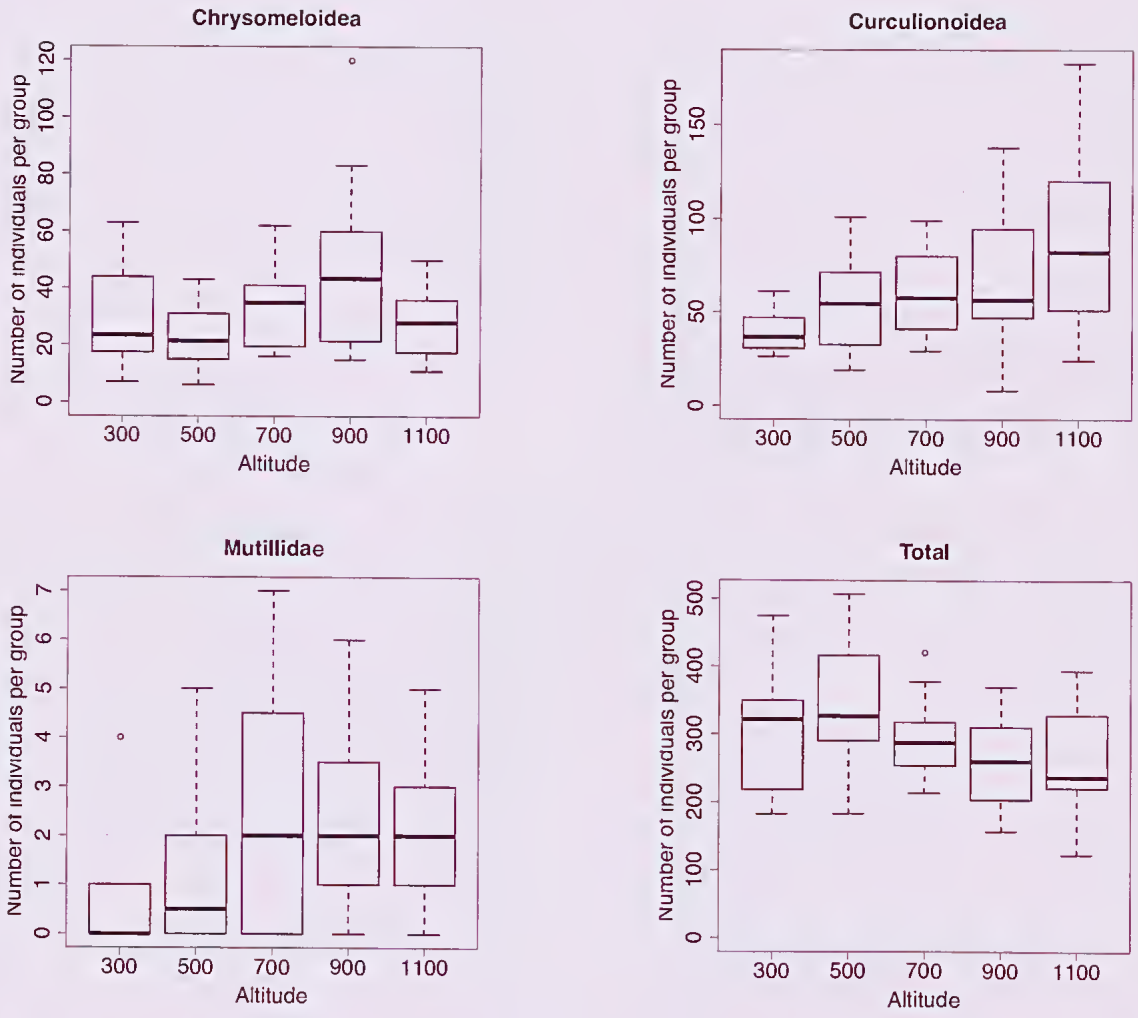


FIG. 3. (This page and opposite) Box-plots of abundances of the nine taxonomic groups and all groups combined ('total') at five different altitudinal zones. The composite group 'other Polyphaga' includes the Scarabaeiformia, Elateriformia, Bostrichiformia and Cleroidea within the Cucujiformia.

tween 16.5 % and 26.4 %. A substantial increase in sampling intensity may be necessary to describe the elevational preferences of all taxa, but singletons found in our study also provide valuable information as many almost certainly prefer the elevation from where they were recorded, based on knowledge of the general feeding habit of the groups to which they belong. The species restricted to higher elevations are generally dominated by moss-feeders and taxa associated with the moist environment in the *Nothofagus*-forest.

The results of the present study may serve as important base-line data upon which predictions can be made in early warning monitoring systems with regard to climatic change. If levels of moisture and precipitation decrease in these forests as predicted from climatic models (Foster 2001), species restricted to certain ranges of altitudes may shift their

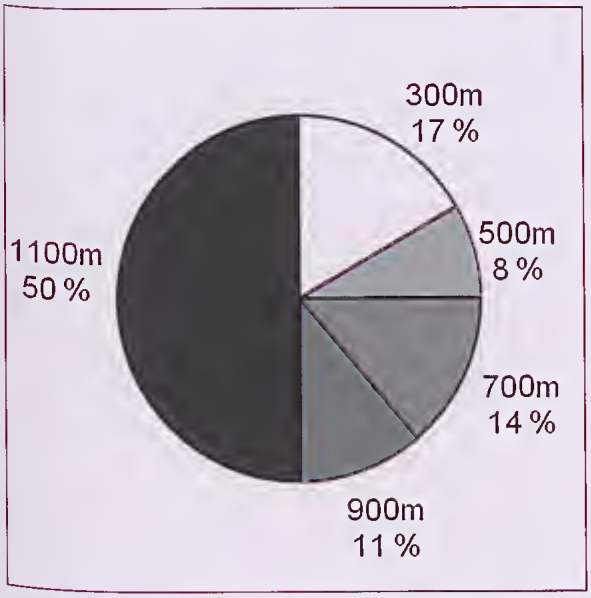


FIG. 4. The proportion of altitude specialists at each of the five altitudinal zones. The data is based on 72 species recorded only from one altitudinal zone, and represented by 5 or more specimens in the total samples.

distribution upwards. These effects may cause loss of high altitude specialists, which has implications for composition and function of the forest ecosystem in the future. In addition, the large proportion and high number of species restricted to high altitudes may have conservation implications as their distributions are already restricted to mountain tops.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. This study was also financially supported by the Norwegian Research Council, the Norwegian Institute for Nature Research. Great thanks to the many volunteers that helped in various phases of field work and with sorting. Thanks to David Putland and Heather Christensen for handling administrative tasks and practical issues during the IBISCA-Queensland project. Thanks also to Oddvar Hanssen for punching the data, and to Åslaug Viken for comments on the manuscript. I am grateful to Roger L. Kitching for encouragement and support throughout this long term study and to Roger and Beverly Kitching for their hospitality during my stays in Australia.

LITERATURE CITED

Andrew, N.R., Rodgerson, L. & Dunlop, M. 2003. Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. *Journal of Biogeography* **30**: 731-746.

Austin, A.D., Yeates D.K., Cassis G., Fletcher M.J., La Salle J., Lawrence J.F., McQuillan P.B., Mound L.A., Bickel D.J., Gullan P.J., Hales D.F. & Taylor G.S. 2004. Insects "Down Under" - Diversity, endemism and evolution of the Australian insect fauna: examples from select orders. *Australian Journal of Entomology* **43**: 216-234.

Basset, Y. 1991. The taxonomic composition of the arthropod fauna associated with an australian rainforest tree. *Australian Journal of Zoology* **39**: 171-190.

2001. Invertebrates in the canopy of tropical rain forests. How much do we really know? *Plant Ecology* **153**: 87-107.

Basset, Y., Novotny V., Miller S.E. & Kitching R.L. 2003. Canopy entomology, an expanding field of natural science. Pp. 4-6. *In*, Basset, Y., Kitching, R.L., Miller, S. & Novotny, V. (eds) *Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy.* (Cambridge University Press: Cambridge).

Bell, K.L., Yeates, D.K., Moritz, C. & Monteith, G.B. 2004. Molecular phylogeny and biogeography of the dung beetle genus *Temnoplectron* Westwood

(Scarabaeidae: Scarabaeinae) from Australia's wet tropics. *Molecular Phylogenetics and Evolution* **31**(2): 741-753.

Brehm, G. & Fiedler, K. 2003. Faunal composition of geometrid moths changes with altitude in an Andean montane rainforest. *Journal of Biogeography*, 30: 431-440.

Cassis, G. & Gross, G.F. 1995. Hemiptera: Heteroptera (Coleorrhyncha to Cimicomorpha). *Zoological Catalogue of Australia.* **27.3A**.

2002. Hemiptera: Heteroptera (Pentatomomorpha). *Zoological Catalogue of Australia.* **27.3B**. Pp 752.

Chen, I-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., Hill, J. K. & Thomas C. D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences* **106**: 1479-1483.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. & Longino, L.T 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**: 258-261.

Didham, R.K. 1997. An overview of invertebrate responses to forest fragmentation. Pp. 303-320. *In*, Watt, A.D., Stork, N.E. & Hunter, M.D. (eds) *Forests and insects*. (Chapman & Hall: London).

Foster, P. 2001. The potential negative impact of globalclimate change on tropicalmontane cloud forests. *Earth-Science Review* **55**: 73-106.

Grimbacher, P.S. & Stork, N.E. 2007. Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest. *Austral Ecology* **32**: 77-85.

Grove, S.J. 2002. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation* **104**: 149-171.

Huston, M. & Gielbert, L.E. 1996. Consumer diversity and secondary production. Pp. 33-47. *In*, Orians, G.H., Dirzo, R. & Cushman, J.H. (eds) *Biodiversity and Ecosystem Processes in Tropical Forests.* (Springer: Berlin).

Hågvar S. 1976. Altitudinal zonation of the invertebrate fauna on branches of birch (*Betula pubescens* Ehrh.). *Norwegian Journal of Entomology* **23**: 61-74.

Janzen, D.H., Ataroff, M., Farinas, M., Reyes, S., Rincon, N., Soler, A., Soriano, P. & Vera, M. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8: 193-203.

Kitching, R.L. & Arthur, M. 1993. The biodiversity of arthropods from Australian rainforest canopies: summery of projects and impact of drought. *Selbyana* **14**: 29-35.

Kitching, R.L., Li. D. & Stork, N.E. 2001. Assessing biodiversity 'sampling packages': how similar are arthropod assemblages in different tropical rainforests? *Biodiversity and Conservation* **10**: 793-813.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland. Project. *Memoirs of the Queensland Museum-Nature* 55(2): 235-250.

Lawrence, J.F. & Britton, E.B. 1994. *Australian Beetles.* (Melbourne University Press: Carlton).

Lawrence, J.F., Hastings, A.M., Dallwitz M.J., Paine T.A. & Zurcher E.J. 2000. *Beetles of the World.* (CSIRO: Collingwood).

MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species.* (Harper & Row: New York).

Moritz, C., Richardson, K.S, Ferrier, S., Monteith, G.B., Stanisic, J., Williams, S.E. & Whiffin, T. 2001. Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota . *Proceedings of the Royal Society London* B **268**: 1875-1881.

Naumann, I.D. 2000. *The insects of Australia: a textbook for students and research workers (2nd edition).* (Melbourne University Press: Melbourne).

Olson, D.M. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* **10**: 129-150.

R Development Core Team. 2008. R: A language and environment for statistical computing. (Royal Foundation for Statistical Computing: Vienna).

Stevens, G.C. 1992. The elevational gradient in altitudinal range: an extention of Rapoport's latitudinal rule to altitude. *The American Naturalist* **140**: 893-911.

Stork, N.E., Balston, J., Farquhar, G.D., Franks, P.J., Holtum, J.A.M. & Liddell, M.J. 2007. Commentry: Tropical rainforest canopies and climate change. *Austral Ecology* **31**: 105-112.

Stork N.E. & Brendell M.J.D. 1990. Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. Pp. 173-190. *In*, Knight, W.J. & Holloway, D.J. (eds) *Insects and the Rain Forest of South East Asia (Wallacea).* (Royal Entomological Society of London: London).

Stork N.E. & Grimbacher P.S. 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society of London B* 273: 1969-1975.

Watt, A.D., Stork N.E., Eggleton, P., Srivastava, D., Bolton, B., Larsen, T.B., Brendell, M.J.D. & Bignell D.E. 1997. Impact of forest loss and regeneration on insect abundance and diversity. Pp. 273-286. *In*, Watt, A.D., Stork, N.E. & Hunter, M.D. (eds) *Forests and insects*. (Chapman & Hall: London).

Williams, J.B., Harden, G.J. & Mc Donald, W.J.F. 1984. Trees & Shrubs in Rainforests of New South Wales & Southern Queensland: Botany (Department of the University of New England: Arimdale).

Wilson, R.D., Trueman, J.W.H., Williams, S.E. & Yeates, D.K. 2007a. Altitudinally restricted communities of schizophoran flies in Queensland's wet tropics: Vulnerability to climate change. *Biodiversity and Conservation* **16**: 3163-3177.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J. 2007b. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology **13**(9): 1873-1887.

Yeates D.K., Harvey M.S. & Austin A.D. 2003. New estimates for terrestrial arthropod species-richness in Australia. *Records of the South Australian Museum Monograph Series* **7**: 231-241.

APPENDIX 1.

Summary of numbers of individuals (ind.) and species (spp.) collected from five different elevations in Lamington National Park (Qld, Australia). Taxonomic resolution is at the family level for most groups and subfamilies for large families. Some groups of Hemiptera are presented at the level of superfamily.

	Sum		300 m		500		700 m		900 m		1100 m	
Group	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.
HEMIPTERA												
Peloridiidae	1	1	0	0	0	0	0	0	0	0	1	1
Enicocephalidae	7	2	0	0	0	0	0	0	0	0	7	2
Schizopteridae	13	2	0	0	1	1	1	1	1	1	10	1
Dipsocoroidea	4	2	0	0	2	2	2	1	0	0	0	0
Reduviidae	24	8	9	6	8	4	6	3	1	1	0	0
Anthocoridae	73	7	8	4	12	5	37	4	15	3	1	1
Tingidae	176	10	31	6	43	6	26	5	72	2	4	2
Miridae	52	12	6	5	8	4	29	8	8	4	1	1
Lygaeidae	265	24	25	2	21	6	8	5	110	9	101	18
Coreidae	9	2	5	1	2	1	1	1	1	1	0	0
Pyrrocoroidea	17	4	7	3	3	3	7	2	0	0	0	0
Berytidae	4	1	0	0	0	0	4	1	0	0	0	0
Aradidae	50	6	21	4	16	4	10	3	3	3	0	0
Pentatomoidea	20	11	8	7	1	1	4	4	4	3	3	2
Total	715	92	120	38	117	37	135	38	215	27	128	28
COLEOPTERA												
Carabidae	264	22	62	8	77	10	34	7	27	8	64	9
Hydrophilidae	110	3	0	0	0	0	0	0	93	2	17	2

APPENDIX 1. continued ...

	Sum		300 m		500		700 m		900 m		1100 m	
Group	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.
Histeridae	5	3	0	0	1	1	2	2	0	0	2	2
Hydraenidae	1	1	1	1	0	0	0	0	0	0	0	0
Ptiliidae	3	3	0	0	1	1	0	0	1	1	1	1
Leiodidae	41	6	0	0	3	2	1	1	29	3	8	2
Scydmaenidae	192	33	10	3	45	12	39	11	43	11	55	15
Staphylinidae	3593	101	1004	24	1227	36	574	30	331	50	457	48
Scaphidinae	35	15	4	4	6	4	6	3	6	5	13	5
Pselaphinae	61	21	0	0	4	4	1	1	17	6	39	15
Scarabaeoidea	19	8	7	4	7	5	5	4	0	0	0	0
Scirtidae	62	11	0	0	7	3	12	6	3	2	40	5
Clambidae	15	3	2	2	0	0	1	1	9	2	3	1
Ptilodactylidae	7	3	1	1	5	3	0	0	1	1	0	0
Buprestidae	6	5	0	0	3	2	1	1	0	0	2	2
Byrrhidae	74	3	0	0	0	0	0	0	1	1	73	2
Limnicidae	20	1	6	1	8	1	5	1	1	1	0	0
Psephenidae	1	1	0	0	0	0	1	1	0	0	0	0
Eucnemidae	8	5	5	2	0	0	1	1	1	1	1	1
Throscidae	15	2	5	1	2	1	7	2	1	1	0	0
Elateridae	717	38	135	17	208	19	153	19	209	13	12	6
Lycidae	28	10	8	5	6	4	10	7	2	1	2	2
Cantharidae	222	18	13	5	24	8	13	5	65	7	107	6
Dermestidae	1	1	0	0	0	0	0	0	0	0	1	1
Anobiidae	45	12	5	3	9	6	8	4	3	2	20	2
Cleridae	58	13	32	8	4	3	16	9	3	2	3	1
Trogossidae	5	3	2	1	1	1	2	2	0	0	0	0
Dasytidae	226	15	30	6	89	6	56	6	44	4	7	5
Malachidae	46	6	9	2	7	2	19	5	11	3	0	0
Nitidulidae	217	17	108	6	54	7	25	6	7	4	23	6
Cybocephalinae	25	5	3	3	3	3	7	3	12	3	0	0
Monotomidae	2	1	1	1	1	1	0	0	0	0	0	0
Phloeostichidae	27	4	0	0	0	0	1	1	1	1	25	4
Silvanidae	121	4	19	3	58	3	42	2	2	2	0	0
Cucujidae	1	1	0	0	0	0	1	1	0	0	0	0
Laemophloeidae	49	4	6	2	15	3	9	3	6	2	13	2
Phalacridae	133	14	51	9	34	8	29	5	17	6	2	2
Cryptophagidae	609	9	90	4	153	6	184	6	69	5	113	6
Erotylidae	49	2	3	1	25	1	10	2	10	1	1	1
Biphyllidae	28	3	4	1	16	3	6	1	1	1	1	1
Cerylonidae	9	3	1	1	2	1	2	1	1	1	3	2
Bothrideridae	6	4	3	3	0	0	3	3	0	0	0	0
Endomychidae	94	8	24	5	29	4	18	3	20	2	3	2

APPENDIX 1. continued ...

	Sum		300 m		500		700 m		900 m		1100 m	
Group	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.
Coccinellidae	713	49	187	15	97	22	238	24	92	18	99	17
Corylophidae	1425	34	324	18	572	23	367	22	99	20	63	12
Latridiidae	508	22	132	13	102	12	106	11	53	10	115	7
Mycetophagidae	16	5	3	2	5	3	5	4	1	1	2	1
Ciidae	11	5	2	2	0	0	1	1	5	3	3	1
Melandryidae	58	14	14	4	16	7	9	3	5	3	14	7
Mordellidae	137	7	63	4	16	3	33	2	25	2	0	0
Rhipiphoridae	3	3	2	2	1	1	0	0	0	0	0	0
Zopheridae	72	10	11	3	5	2	14	6	5	4	37	4
Tenebrionidae	266	19	10	5	26	12	38	12	20	8	172	4
Lagrinae	1	1	0	0	1	1	0	0	0	0	0	0
Alleculinae	138	14	17	5	21	8	59	8	35	8	6	3
Prostomidae	1	1	0	0	0	0	0	0	1	1	0	0
Oedemeridae	3	3	2	2	0	0	1	1	0	0	0	0
Pythidae	7	1	0	0	5	1	2	1	0	0	0	0
Pyrochroidae	45	7	5	1	3	3	10	5	26	3	1	1
Salpingidae	20	4	0	0	4	2	8	3	4	1	4	2
Anthicidae	262	8	202	4	45	3	10	5	2	2	3	2
Aderidae	151	27	42	12	39	11	56	16	12	8	2	2
Scraptidae	36	6	14	3	9	2	12	3	1	1	0	0
Cerambycidae	331	55	115	36	46	15	122	26	37	20	11	7
Chrysomelidae												
Megalopodinae	5	3	0	0	1	1	1	1	1	1	2	1
Clytrinae	9	4	0	0	0	0	8	3	0	0	1	1
Chrysomelinae	249	33	38	9	64	15	69	20	48	17	30	8
Eumolpinae	47	12	10	3	8	5	6	3	18	5	5	2
Galerucinae	516	25	195	15	133	15	147	15	35	11	6	3
Alticinae	792	31	5	4	25	11	52	7	434	14	276	21
Cassidinae	9	2	2	1	1	1	4	2	1	1	1	1
Anthribidae	245	39	35	17	63	22	51	19	73	19	23	6
Attelabidae	53	9	16	3	10	3	11	4	12	3	4	2
Nemonychidae	9	2	1	1	6	2	2	1	0	0	0	0
Belidae	6	3	5	2	0	0	1	1	0	0	0	0
Brentidae	15	7	1	1	2	2	8	4	3	2	1	1
Apionidae	34	11	6	3	1	1	4	3	8	5	15	3
Curculionidae												
Otiorynchinae	375	16	60	5	34	2	28	7	132	8	121	7
Curculinoninae s.l.	1160	91	148	36	304	34	229	45	199	24	280	27
Hylobiinae	24	4	9	3	4	1	8	3	3	2	0	0
Magdalinae	31	6	2	2	8	4	21	3	0	0	0	0

APPENDIX 1. continued ...

	Sum		300 m		500		700 m		900 m		1100 m	
Group	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.
Cossoninae	54	13	8	5	2	2	5	2	15	7	24	5
Cryptorhynchinae	1588	156	143	44	169	53	335	74	365	71	576	64
Platypodinae	1	1	1	1	0	0	0	0	0	0	0	0
Scolytinae	107	11	32	6	35	5	19	5	14	3	7	2
Total	16783	1219	3516	429	4017	484	3404	541	2831	461	3015	383
HYMENOPTERA												
Mutillidae	105	17	7	5	14	6	31	7	28	8	25	5
Total of all groups	17603	1328	3643	472	4148	527	3570	586	3074	496	3168	416

Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest - exploring indicators of climate change

Louise A. ASHTON

Roger L. KITCHING

Sarah C. MAUNSELL

Darren BITO

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email:l.ashton@griffith.edu.au

David A. PUTLAND

Growcom, PO Box 202, Fortitude Valley Qld 4006, Australia.

Citation: Ashton, L.A., Kitching, R.L., Maunsell, S.C., Bito, D. & Putland, D.A. 2011 12 20: Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest - exploring indicators of climate change. *Memoirs of the Queensland Museum — Nature* 55(2) 375-389. Brisbane. ISSN 0079-8835.

ABSTRACT

Moth assemblages have been widely used to estimate patterns of beta-diversity in forest ecosystems. As part of the IBISCA-Queensland project we examined patterns of diversity in a large subset of night-flying moths along an altitudinal gradient in subtropical rainforest. The permanent IBISCA-Queensland transect located in Lamington National Park, south-east Queensland, Australia, spans altitudes from 300 metres (m) to 1100 m above sea level (a.s.l.) within continuous, undisturbed rainforest. We sampled four replicate plots at each of five altitudes (300, 500, 700, 900, 1100 m a.s.l.). A total of 11379 individual moths were sampled, belonging to approximately 865 morphospecies. Moth assemblages displayed a strong altitudinal signal at each of two sampling periods (October 2006 and March 2007). The results show that cloud forest above 900 m a.s.l. where *Nothofagus moorei* becomes dominant, contains a number of moth species that are restricted to the high elevation forest and these species may be most threatened by climatic change. The analyses presented here suggest a set of 18 moth species which may be useful as part of a multi-taxon predictor set for future monitoring of the impact of global warming on forest biodiversity. ❐ *climate change, subtropical, rainforest, IBISCA, Lepidoptera.*

Climate change is having a marked effect on terrestrial ecosystems, as evidenced by poleward and elevational shifts in the distributions of many species of plants and animals (Bale *et al.* 2002; Grabherr *et al.* 1994; Hickling *et al.* 2006; IPCC 2007; Parmesan 1996). The IBISCA-Queensland project aimed to quantify the relationship between climate and biodiversity along an altitudinal gradient in subtropical rainforest and, by so doing, develop robust measures for future monitoring of climate change impacts (Kitching *et al.*, 2011). This paper investigates moth assemblages along this altitudinal gradient, and suggests a group of moth species that may be used to monitor altitudinal shifts in distributions.

It has been predicted that climatic warming over the course of the next century will cause an increase in global average temperature of between 1.4°C and 5.8°C (IPCC 2007). Changes to climatic conditions are likely to result in increased weather variability and extreme weather events (Easterling *et al.* 2000), leading to dramatic changes in ecosystem dynamics (Weltzin *et al.* 2003). The responses of ecosystems to climate change are wide and varied, and are confounded by species interactions and feedback relationships. Species interactions may enable some groups to adapt to new conditions, for example, through shifts in community composition and simplification of food webs (Suttle *et al.* 2007). However, changed conditions may exceed the environmental thresholds for many species leading to changes in distribution or, if this is not possible, local or even global extinction (Pounds *et al.* 1999; Thomas *et al.* 2004). Biological responses due to climate change, such as distribution shifts and phenological changes, have already been measured in a variety of taxa and ecosystems (Parmesan & Yohe 2003; Walther *et al.* 2002).

Studies of altitudinal gradients are an effective method of investigating and monitoring the impacts of climate change because they allow for a wide range of changing environmental variables to be observed over small geographical areas. They provide ideal situations to explore how species distributions may be associated with, and limited by, climatic factors, while minimising confounding historical factors that influence species distributions over latitudinal gradients (Fiedler & Beck 2008; Shoo *et al.* 2006). Altitudinal gradients potentially provide insight into climate change impacts, because they encompass steep temperature and moisture gradients, leading to stratified environmental parameters and faunal assemblages (Hodkinson 2005; Shoo *et al.* 2006). Many studies have shown that montane cloud forests are highly sensitive to, and threatened by, climate change (Foster 2001; Nadkarni & Solano 2002; Pounds *et al.* 1999; Still *et al.* 1999; Williams *et al.* 2003).

A medium-range climate change scenario predicts an average global temperature increase of 4°C over the next 100 years, which would push current climate envelopes around 800 m upwards in altitude (Malhi & Phillips 2004). Even an optimistic climate change scenario predicts upward shifts in climatic envelopes of up to 450 m (Loope & Giambelluca 1998). However, these estimates are likely to vary regionally and will also depend on local conditions. Despite this, the estimates are of particular concern because cloud forest ecosystems often encompass rare and endemic species with limited altitudinal ranges (Foster 2001). Some plant species in tropical montane forests, for example, display ranges of less than 300 m (Loope & Giambelluca 1998).

IBISCA-Queensland was a collaborative, international investigation of patterns of diversity and ecosystem processes along an altitudinal gradient. This study investigated which species are sensitive to climatic variability associated with increasing altitude and therefore most likely to be sensitive to climate change and, by doing so, sought to establish current baseline information, laying the foundation for longer-term monitoring programs. Study sites for this project are located in the UNESCO World Heritage listed Lamington National Park, noted for its isolated patches of montane, Antarctic Beech (*Nothofagus moorei*) dominated, 'cool temperate' rainforest.

The collaborative approach of the IBISCA-Queensland project involved a broad range of taxonomic and ecological specialists each working to a fixed experimental design. This helped ensure that a wide range of taxa were studied, producing a multi-faceted baseline dataset describing a range of invertebrate and plant assemblages. The culmination of the study will be a powerful 'predictor set' (Kitching 1993) that can be re-sampled in the future in order to monitor impacts of climate change. In this paper we examine the potential of moths for inclusion in this predictor set. Monitoring protocols such as those which will be created by this study

will provide important tools for understanding biotic responses to climate change, subsequently facilitating adaptive management strategies that encompass such responses. Moths are potentially particularly useful in this regard because they are diverse, relatively well-known taxonomically and, as herbivores, reflect closely the vegetational health of the forest (Kitching *et al.* 2000; Scoble 1995). They are also sensitive to environmental variables, being strongly affected by temperature and precipitation and resource limiting factors such as food availability (Holloway *et al.* 1992). Moths have been used as indicators of environmental change and the success of restoration in a variety of different terrestrial ecosystems, such as rainforests, temperate forests and agro-ecosystems (Beccaloni & Gaston 1994; Brown & Freitas 2000, New 1997; Ricketts *et al.* 2001).

The current study posed the following two questions by sampling moth assemblages along an altitudinal transect within the subtropical forest of Lamington National Park.

(1) Do moth assemblages change with altitude?

(2) If so, which moth species show the strongest altitudinal signal thus making them potentially appropriate indicators of future climate change within Lamington National Park?

METHODS

Study site

Lamington National Park is a protected area of forests covering 206 km^2 and includes the Lamington Plateau, which is located across the Queensland-New South Wales border, a part of the larger Tweed Caldera region (Willmont 2004). Lamington National Park is part of the Gondwana Rainforests of Australia, a group of eight national parks in south-east Queensland and north-east New South Wales, and has been World Heritage listed since 1994. The area mainly lies upon Cainozoic igneous rock, derived from volcanic eruptions. Lamington Plateau was formed by a now extinct shield volcano, centred at Mount Warning, in north-eastern New South Wales (Stevens 1997).

The altitudinal transect that is the basis of the IBISCA-Queensland project was established in continuous rainforest within the Green Mountains section of Lamington National Park and encompasses a steep temperature and moisture gradient (Strong *et al.* 2011). The transect encompasses altitudes between 300 and 1100 m a.s.l. with four replicate plots located within coarse elevational bands centred upon altitudes of 300, 500, 700, 900 and 1100 m a.s.l. Lower elevation plots (300 and 500 m a.s.l.) are located within the valley of West Canungra Creek. Middle and high elevation plots (700 m a.s.l. and above) are located along the western slopes of the same valley, along the access road to Green Mountains, O'Reilly's Guesthouse and the Border Track leading to Mount Bithongabel. Low altitude plots are characterised by dryer, hotter conditions and the high altitude sites experience lower temperatures and higher moisture levels (Strong *et al.* 2011). The cloud cap, the lower limit of which sits between 800 and 900 m a.s.l depending on season and weather conditions, is likely to have a strong influence on local climate.

The rationale for the overall project and the locations of study plots are presented by Kitching *et al.* (2011). Strong *et al.* (2011) describe the climate and soil conditions prevailing across the selected altitudes. Laidlaw *et al.* (2011) describe vegetation changes along the transect. The low elevation plots at 300 m a.s.l. are classified as complex notophyll vine forest (*sensu* Webb and Tracey 1978) dominated by Hoop Pine (*Araucaria cunninghamii*). The mid-elevation plots, 500, 700 and 900 m a.s.l., are also complex notophyll vine forest (McDonald & Hunter 2008). The highest altitude plots at 1100 m a.s.l. are simple microphyll fern forest dominated by Antarctic Beech (*Nothofagus moorei*).

Moth collection and identification

Trap design. Moths were sampled using modified Pennsylvania light traps (Frost 1957; Kitching *et al.* 2005) fitted with 12 volt gel-cell batteries. Traps employed a vertical actinic tube, producing short wavelength blue light. This tube was surrounded by three transparent vanes that intercepted and knocked down insects attracted to the light into a bucket below. The bucket contained a Sureguard® resin strip impregnated with Dicholorvos™ insecticide which killed moths *in situ*. Traps were set daily and ran for 12 hours from 6 pm to 6 am.

Two Pennsylvania light traps were run simultaneously on a plot on each trapping night, with one trap at ground level and one in the forest canopy. Canopy traps were raised to a height of approximately 35 metres, depending on the height of the canopy, and ground traps were raised a few metres above the ground and hung from a low branch. The light traps were placed at both ground and canopy level to ensure a broader sampling of moth diversity (Brehm 2007; Beck *et al.* 2002; Schulze *et al.* 2001).

Sampling regime. Sampling took place in October 2006 and March 2007. Two traps (ground and canopy) were set simultaneously for three nights at each plot. Traps were emptied daily and all arthropods caught were transferred to sample containers and taken to a field laboratory. In total, 120 samples were collected in the first sampling period, from 14th to 31st October 2006, and 108 samples were collected in the second sampling period, from 10th March to 2nd April 2007. Two of the four 500 m a.s.l. plots were not sampled in March 2007 due to time constraints. In order to minimise the negative effect of moonlight on catches (Muirhead-Thomson 1991; Yela & Holyoak 1997; Nowinszky 2004) no trapping was carried out five days either side of the full moon.

Processing catches. Moths with a wing length of 1 cm or more were processed, thus representing the macrolepidoptera. In addition, all moths belonging to the superfamily Pyraloidea (i.e. the families Crambidae and Pyralidae), regardless of their size, were also processed. This group was targeted in addition to the macrolepidoptera because of the relatively good resources available for the identification of many subgroups within the Pyraloidea (Common 1990).

Based on external characteristics, moths were sorted to species, hereafter referred to as 'morphospecies' and each morphospecies was assigned a unique code number. As sorting proceeded, a reference collection including at least one representative of each morphospecies was assembled. Individuals in a given sample that could be readily identified as belonging to an existing, numbered morphospecies were recorded and discarded. Identification to generic and species level was carried out principally by comparison with the reference collections available in the Queensland Museum, Brisbane, Australia. Identified material from previous surveys in the Lamington region held by the Arthropod Biodiversity Laboratory at Griffith University was also used in addition to printed and electronic resources (Common 1990; www.ento.csiro.au/anic/moths.html).

ANALYSIS.

Data from the paired canopy and ground-level traps across three trap nights were pooled into one dataset for each plot. Quantitative samples of insects are often characterised by zero-inflated data with a small number of very abundant species and this was found to be the case in our samples. Multivariate analyses were based on the proportion of species within samples and these were log transformed in order to reduce the impact of highly dominant species. The multivariate analysis package Plymouth Routines in Multivariate Ecological Research [PRIMER 6™] (Clarke & Gorley 2006) was used to investigate patterns of moth assemblages across altitudinal zones.

Permutational multivariate analysis of variance (PERMANOVA) was conducted in PRIMER 6 with PERMANOVA+ add-on software (Anderson *et al.* 2008), testing for significant differences in the moth assemblage composition among a number of *a priori* groups, in this case the five

altitudinal bands. This analysis was run with 9999 permutations, using the Bray-Curtis dissimilarity measure (Bray & Curtis 1957). The pair-wise post-hoc comparisons of each altitudinal group were used here to explore differences between altitudinal bands. Owing to time constraints, in the October 2006 sampling session, only three of the 300 m a.s.l. sites were sampled, and in March 2007 only two of the 500 m a.s.l. sites were sampled. Because of this discrepancy pair-wise comparisons between altitudes for the 500 m sites in the March 2007 have been excluded to avoid unbalanced replication.

The Bray-Curtis dissimilarity measure (Bray & Curtis 1957) was also used to create a distance matrix. From this matrix, non-metric multi-dimensional scaling (NMDS), set to 100 random starts, was used to produce ordination plots illustrating the relationship of moth assemblages among sampling sites. The NMDS approach to analysis has been adopted successfully in similar studies of moths, and is useful in detecting patterns in assemblages that tend toward high diversity and low evenness (Beck & Chey 2008; Brehm & Fiedler 2004; Fielder *et al.* 2008).

Relationships between environmental variables and overall moth assemblage composition were investigated using the Distance-based Linear Model (DistLM) function in PERMANOVA+. Marginal tests available within the DistLM procedure investigate which environmental variables are significantly correlated to the variation in moth assemblage composition. The vectors of significant environmental variables were then superimposed on NMDS ordinations of moth assemblages. The length of vectors indicates the strength of the correlation and their direction indicates whether the environmental variables were positively or negatively correlated with the observed patterns of assemblage composition. Environmental vectors which were measured as part of the IBISCA-Qld project included soil moisture, soil organics, tree species richness and median temperature. The methods of collection of this environmental data are summarised by Strong *et al.* and Laidlaw et al. (2011). A metric called 'fog events' was also used, indicating days when weather data recorders showed periods of 100% atmospheric humidity, thought to reflect fog events, although some inaccurate readings may result from the data loggers being wet from rainfall.

We also investigated the extent of variation in moth assemblage explained by spatial-auto correlation, in comparison to altitudinal differences. To this end, latitudes and longitudes of the site locations were first centred and rotated using PCA ordination with PRIMER 6, and the resultant x and y coordinates were used to generate a between-site distance matrix based on Euclidean distance measures. Similarly, another distance matrix (based on Euclidean distance measures) was generated using altitudinal differences between sites. Two separate Mantel tests (available from the RELATE routine within PRIMER 6) were conducted to calculate correlation coefficients and associated *P* values between distance matrices of moth assemblages and site locations, and moth assemblages and altitudinal differences.

RESULTS

A total of 11 379 moths belonging to 865 morphospecies was sampled in this study; 3490 individuals in October 2006 and 7889 in March 2007. Samples collected in October 2006 showed a mid-elevation peak in species richness which was highest at 500 m a.s.l. No such peak was apparent in the March 2007 data, although it should be noted that sampling effort at 500 m a.s.l. in March 2007 was restricted to two sites.

Ordination plots of moth assemblages sampled in October 2006 (Fig. 2a) and March 2007 (Fig. 2b) show a clear altitudinal signal in assemblage structure between 300 and 1100 m a.s.l. The PERMANOVA analysis indicated a highly significant relationship between altitude and moth assemblages for both the October 2006 (pseudo-*F*

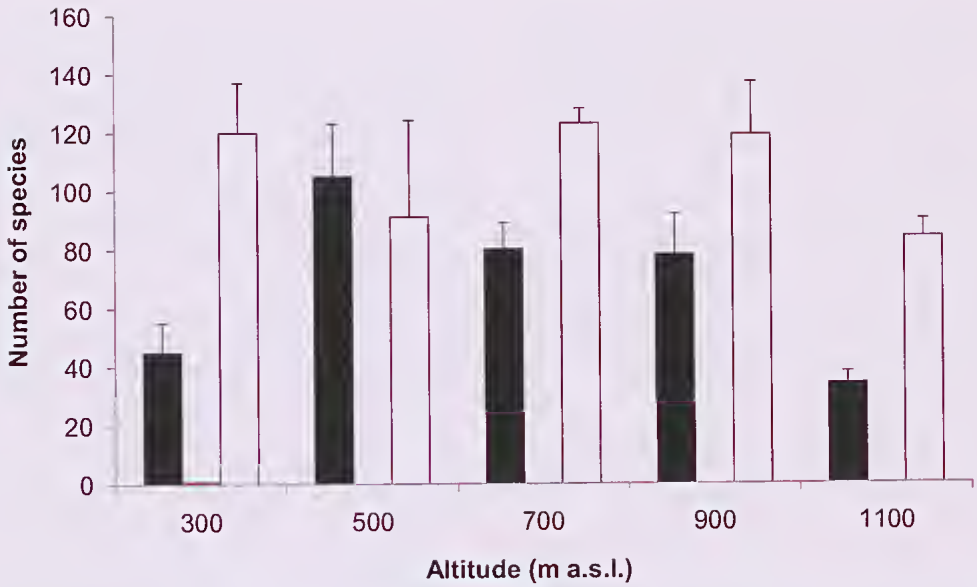


FIG. 1. Mean moth species richness (+ 1 x standard deviation) at each sampled elevation in October 2006 (black bars) and March 2007 (open bars). In March 2007, only two of the four 500 m a.s.l plots were sampled, therefore the complete range is shown for this sampling occasion.

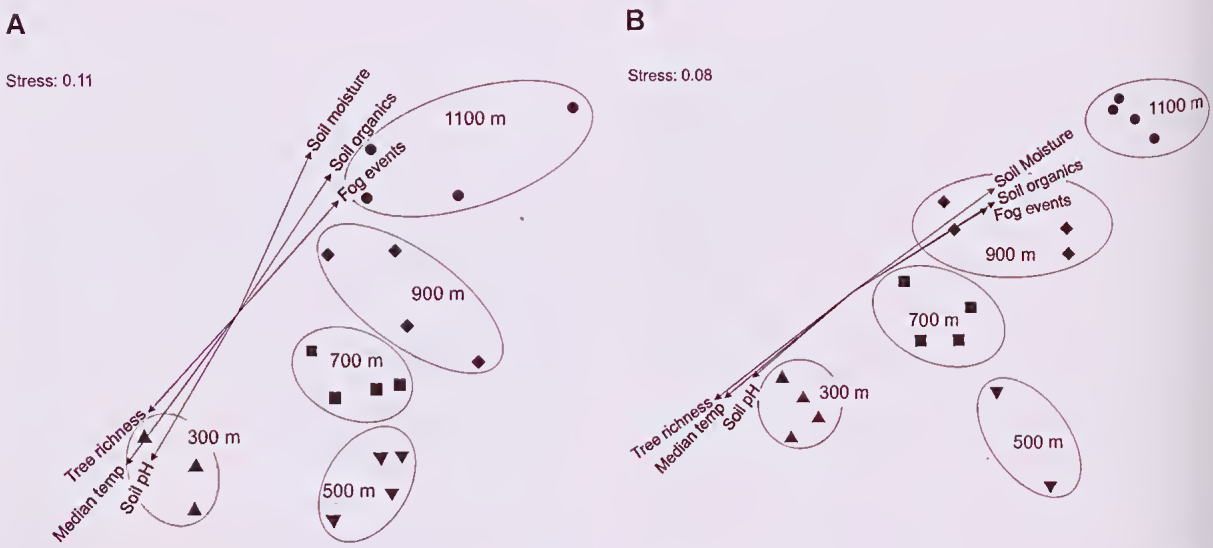


FIG. 2. NMDS ordination plots of moth assemblages, based on log transformed proportion of morpho-species, collected in (a) October 2006 and (b) March 2007. Only three of the 300 m a.s.l. plots were sampled in October 2006, and only two of the 500 m a.s.l. plots during March due to time constraints. Superimposed vectors are environmental parameters significantly correlated to the assemblage composition.

TABLE 1. Results of pair-wise post-hoc comparisons of moth assemblages between altitudinal (m a.s.l.) groups for October 2006 and March 2007 (500 m sites have been excluded from March 2007 analysis due to low replication), showing degrees of freedom (df), *t* and *P* values. Analyses were based on log transformed proportions of morphospecies.

	October 2006			March 2007		
Comparison	df	*t*	*P*	df	*t*	*P*
300 and 500 m	5	1.85	0.030	-	-	-
300 and 700 m	5	1.83	0.029	6	2.32	0.028
300 and 900 m	5	2.02	0.028	6	2.35	0.029
300 and 1100 m	5	2.02	0.026	6	3.55	0.031
500 and 700 m	6	1.28	0.057	-	-	-
500 and 900 m	6	1.69	0.030	-	-	-
500 and 1100 m	6	2.02	0.029	-	-	-
700 and 900 m	6	1.26	0.062	6	1.60	0.028
700 and 1100 m	6	1.69	0.030	6	2.86	0.028
900 and 1100 m	6	1.39	0.025	6	2.05	0.026

TABLE 2. Average similarities between and within altitudinal (m a.s.l.) groups, based on log transformed proportions of morphospecies, from four plots at each altitudinal band collected in (a) October 2006 and (b) March 2007.

a) Collection from October 2006

	300 m	500 m	700 m	900 m	1100 m
300 m	44.89				
500 m	24.23	40.16			
700 m	21.89	33.36	36.34		
900 m	16.18	25.60	32.24	37.27	
1100 m	12.96	14.45	19.95	27.23	32.03

b) Collection from March 2007

	300 m	500 m	700 m	900 m	1100 m
300 m	50.83				
500 m	20.14	38.30			
700 m	22.12	27.79	42.23		
900 m	16.43	23.01	28.12	36.03	
1100 m	07.73	11.77	14.06	26.44	56.23

= 2.95, P = 0.001) and March 2007 datasets (pseudo-F = 5.13, P = 0.0001). Pair-wise post-hoc comparisons, testing between each of the altitudinal groups (Table 1), showed that most altitudinal groups were significantly different from each other, with the exception of 500 and 700 m, and 700 and 900 m, but only in the October 2006 results, when fewer moths were collected.

Marginal tests within the DistLM routine showed the same six environmental variables significantly correlated with moth assemblages collected in both October 2006 and March 2007. Changes in moth assemblages with increasing altitude were positvely correlated to soil moisture (October, F = 3.6, P = 0.0001; March, F = 6.4, P = 0.0001), soil organic content (October, F = 3.2, P = 0.0001; March, F = 5.5, P = 0.0001) (presumably reflecting slower breakdown processes induced by lower temperatures) as well as fog events (October, F = 2.6, P = 0.0004; March, F = 5.2, P = 0.0001) (100% atmospheric humidity, from which we may infer a higher frequency of fog events and rainfall), whereas reverse trends were found for median temperature (October, F = 3.7, P = 0.0001; March, F = 6.5, P = 0.0001), soil pH

TABLE 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park based on combined data from samples taken in October 2006 and March 2007. Only species that were represented by 30 or more individuals included. The black bars indicate the altitude or range of altitudes at which at least 80% of the total number of individuals were restricted.

Species	Family	Subfamily	Fig.	Altitude (m a.s.l.) 300 500 700 900 1100
Termessa gratiosa	Arctiidae	Lithosiinae	3A	
Rhimphalea sceletalis	Crambidae	Pyraustinae	3B	
Lyclene structa	Arctiidae	Lithosiinae	3C	
Asura cervicalis	Arctiidae	Lithosiinae	3D	
Eustixis laetifera	Lacturidae		3E	
Palaeosia bicosta	Arctiidae	Lithosiinae	3F	
Ectropis bispinaria	Geometridae	Ennominae	3G	
Hesychopa chionora	Arctiidae	Lithosiinae	3H	
Xylodryas leptoxantha	Geometridae	Ennominae	3I	
Aboetheta pteridonoma	Crambidae	Pyraustinae	3J	
Eurychoria fictilis	Geometridae	Ennominae	3K	
Lyelliana dryophila	Geometridae	Ennominae	3L	
Laroplylla amimeta	Geometridae	Ennominae	3M	
'Dyscheralcis' crinnodes	Geometridae	Ennominae	3N	
Heterochasta conglobata	Geometridae	Larentiinae	3O	
Lychnographa heroica	Geometridae	Ennominae	3P	
Thalatha trichroma	Noctuidae	Amphipyrinae	3Q	
Middletonia hemichroma	Geometridae	Ennominae	3R	

(October, $F = 3.4$, $P = 0.0001$; March, $F = 5.0$, $P = 0.0001$) and tree species richness (October, $F = 1.7$, $P = 0.027$; March, $F = 2.8$, $P = 0.007$) (Figures 2a and 2b).

Mantel tests showed a high correlation between moth assemblages and altitude (correlation coefficient (Rho) of 0.84, $P < 0.002$ in March, and Rho = 0.73, $P < 0.001$ in October). However, moth assemblages were also equally highly correlated with the geographic arrangement of the sites (Rho = 0.85, $P < 0.001$ in March, and Rho = 0.728, $P < 0.001$ in October).

The moth assemblages of plots at 1100 m a.s.l. were clearly differentiated from those at other elevations, particularly in the March sample (Fig. 2b), and featured a number of moth species not found at lower elevations. The average similarity between altitudinal groups, summarised in Table 2, demonstrates decreasing assemblage similarity with increasing distance between altitudinal groups, indicating strong altitudinal turnover of moth assemblages with altitude.

Species with altitude-restricted distributions

As a first step towards nominating which species might be useful as indicators of climate change at particular elevations, or ranges of elevations, and hence promising candidates for future monitoring, we identified species with restricted altitudinal distributions (Table 3). For this we selected species represented by at least 30 specimens with at least 80% of the catch restricted to one or a small range of altitudes. In total there were 28 such taxa, 18 of which we have thus far been able to identify with confidence to species level. Of these 18 species (and using the 80% criterion mentioned above) nine were

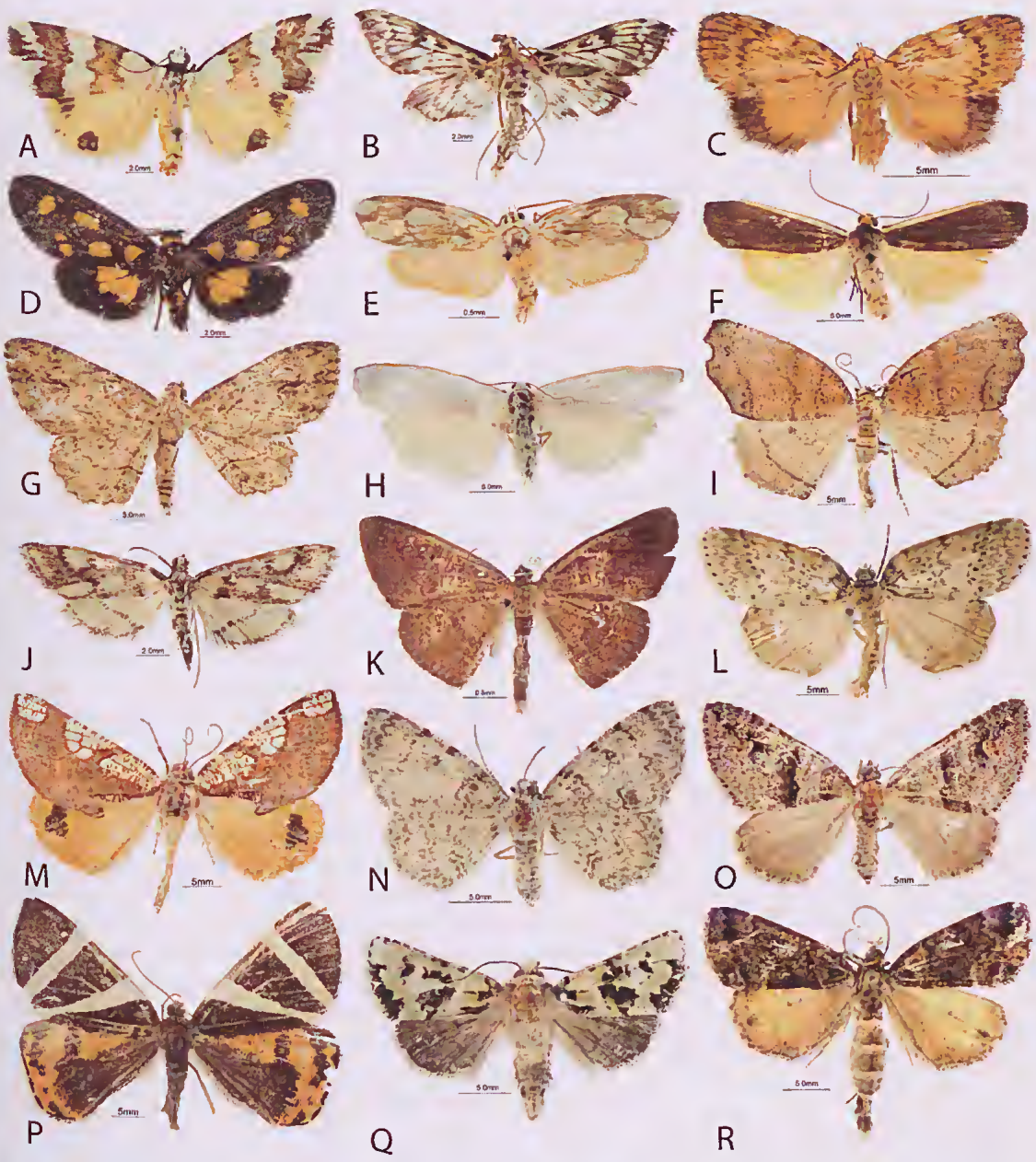


FIG. 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park (see Table 3 for family and subfamily placements). A, *Termessa gratiosa* (Walker); B, *Rhimphalea sceletalis* Lederer; C, *Lyclene structa* (Walker); D, *Asura cervicalis* Walker; E, *Eustixis laetifera* (Walker); F, *Palaeosia bicosta* (Walker); G, *Ectropis bispinaria* (Guenée); H, *Hesychopa chionora* (Meyrick); I, *Xylodryas leptoxantha* (Turner); J, *Aboetheta pteridonoma* Turner; K, *Eurychoria fictilis* (Turner); L, *Lyelliana dryophila* Turner; M, *Larophylla amimeta* Turner; N, *'Dyscheralcis' crinnodes* (Turner); O, *Heterochasta conglobata* (Walker); P, *Lychnographa heroica* Turner; Q, *Thalatha trichroma* (Meyrick); R, *Middletonia hemichroma*. (Turner).

characteristic of a single altitude; three to 300 m, one to 700 m and five to 1100 m a.s.l. A further six species were commonly spread over two altitudes; one from 700 – 900 m and five from 900 – 1100 m a.s.l. Finally, three species occupied less restricted altitude ranges; one from 300 – 700 m and two from 700 – 1100 m a.s.l. These altitudinally restricted species represented five families. The 'lower elevation species', those characteristic of plots from 300 to 700 m a.s.l., comprised three lithosiine arctiids and a single pyraustine crambid. In contrast, species characteristic of higher elevations (900 –1100 m a.s.l.) were principally geometrids (nine ennomines and one larentiine) with one amphipyrine noctuid and a pyraustine crambid. Species restricted to mid-elevations (500–700 m a.s.l.) were, in general, scarce. The two species we identified in this category comprised a lithosiine arctiid and the lacturid, *Eustixis laetifera*.

DISCUSSION

The main objective of this study was to document changes in moth assemblages along an altitudinal gradient within continuous rainforest. We have demonstrated that there are characteristic assemblages of species at each elevation in two seasons and have identified particular species with indicator potential. In this discussion we examine potential explanations for these patterns and the potential impacts of climate change upon them. We discuss the likely generality of our results and avenues for further research.

The occurrence of a species in a particular sample results from a multiplicity of factors. These may be methodological or biological. Methodologically we acknowledge that we are sampling only night-flying, light-attracted moths. This is a subset of all moths but, nevertheless, is sufficiently large to provide a degree of confidence to identify community patterns from which usable management tools can be derived. Light traps are relatively easy to use and produce large samples. Poor catches can result from their use on cold and/or windy nights and bright moonlight undoubtedly adversely affects catches on clear nights (Nowinszky 2004). Any moth trapping programme must be flexible enough to substitute additional sampling nights in response to the occasionally unsuccessful trap night. A more serious issue concerning the repeatability and representativeness of light-trap samples is that of seasonality. There are undoubtedly different assemblages of moth species flying at different times of the year. Further, even for a particular species, there will be a peak time of flight activity and the first emergents or last survivors of a species, appearing in trap catches, may give a false impression of rarity. We have partly addressed this problem by sampling on two different occasions (and a third not reported on here). Nevertheless, any comparisons using results of the kind we have reported must aim to target a comparable season. Of course, year-long sequences of catches would be useful in resolving the issue of seasonality across species. There are, however, no such datasets available for any subtropical Australian location. Even where such datasets available, the highly variable Australian climate would, quite possibly, prevent the drawing of general conclusions concerning species diversity from a single year's data. We suggest the large sample sizes and the fact that rather similar patterns emerged from two quite different sampling periods lends a good deal of credibility to the conclusions. We note also that singletons or doubletons (i.e. species that appear only once or twice within our samples) had little impact on the results of multivariate ordinations (results not presented here).

Ecologically, the presence or absence of a particular species at a particular elevation will be determined by the limiting dimensions of the niche of each species. These may be physico-chemical dimensions such as temperature, moisture and soil chemistry, or biological variables based on interactions with food-plants, competitors and natural predators. The physico-chemical variables are dimensions of the fundamental niche of the species and reflect the evolved physiological tolerances of the species concerned. Biological

interactions add dimensions to the niche space which define the realised niche of the species and usually define a hypervolume nested within that circumscribed by the fundamental niche dimensions (Hutchinson 1957). We say 'usually' because, in rare instances, mutualistic interactions may expand the niche of a species beyond the volume defined by its physiological tolerances to physio-chemical factors. It would be in line with general niche theory (see for example Dobzhansky 1950; McCoy 1990) to suppose that species restricted to altitudes presenting more extreme and challenging microclimates, would be more likely to be restricted by their physiological tolerances of climatic extremes, whereas those species spread across altitudes, presumably comfortably within their physiological envelopes, are more likely to be restricted by biological interactions. Biological interactions that may restrict the spatial distribution of moths are likely to include the presence or absence of acceptable food-plants and the suite of predators and parasitoids co-occurring with them.

Our nomination of moth species which may be useful as indicators is preliminary. As other species are firmly identified, so additional, usable, range-restricted species can be added to the list. Further statistical characterisation of the 'attachment' of these species to particular altitudinal ranges is in progress. Of course, one set of information that would assist in explaining these patterns are lists of the larval food plants of these species. Very little published information is available on this subject (www-staff.it.uts.edu.au/~don/larvae). There is general agreement that larvae of many lithosiines feed on lichens and this has been confirmed for *Termessa gratiosa* and *Palaeosia bicosta*. Given that montane and boreal lichen distributions are predicted to shift under climate change (Ellis *et al* 2007), these species feeding on lichens may be of conservation concern.

There is published food-plant data available for only one of the remaining species, *Ectropis bispinaria* (Geometridae: Ennominae), which is highly polyphagous, being recorded from species of Rutaceae, Lauraceae, Rosaceae and Proteaceae with all families being well represented in the flora of the Lamington rainforest. Larval rearing by one of us (D. Bito) adds Monimiaceae (*Daphnandra micrantha*) and Sapindaceae (*Arytera divaricata* and *A. dystilis*) to this list. Other species within the lacturid genus *Enstixis* have been reared from *Ficus* spp. and this association might reasonably be expected for *E. laetifera*. Unpublished rearing records provide a few additions. Among the ennomines, *Middletonia hemichroma* has been reared from *Nothofagus moorei* (Nothofagaceae), *Quintinia verdonii* (Quintiniaceae) and *Syzygium crebrinerve* (Myrtaceae); and *Dyscheralcis crimmodes* has been reared from *Neolitsea australiensis* (Lauraceae) and *Pentaceras australis* (Rutaceae) (D. Bito, unpub. data).

Testing these explanatory hypotheses related to the altitidinal distributions of species is restricted by insufficient data on both host plants and natural enemies. We have some, albeit sparse, data on food-plants but we have virtually no information on parasitoid loads. Both deficiencies point to likely rewarding future areas of investigation. The IBISCA-Qld Project has generated substantial samples of micro-Hymenoptera through Malaise trapping (see Boulter *et al.*, this issue) and further analysis of these samples may provide more insight into their likely significance in structuring moth assemblages.

The existence of clear cut patterns of altitudinally delimited moth assemblages, with particular species having clearly restricted altitudinal distributions, suggests that selected moth taxa will be useful in tracking any upward shifts in distribution and invasions of higher altitudes – a likely consequence of global warming. It also suggests that the highly distinctive upper elevation assemblage must be regarded as vulnerable and of conservation concern. The patterns we have identified are concordant with studies of other taxa that formed part of

the IBISCA-Qld Project and with other studies of moths on altitudinal gradients elsewhere (Fiedler *et al.* 2008; Brehm & Fiedler 2003). Our results suggest that the most sensitive altitudes to target for monitoring in the relatively short-term (say over 20-30 years) will be those at 700 m a.s.l. and above, where cloud base fluctuations are predicted to alter ecosystem structure and dynamics (Laidlaw *et al.* this issue). This conforms with the opinions of earlier authors who have suggested that such ecotones are the areas that will show the strongest signals of climate change (Parmesan & Yohe 2003).

The selection of suitable indicator species depends on several criteria. An effective indicator needs to be present in large numbers, be easily recognisable, as well as being sensitive to environmental variables (Holloway 1998; Scoble 1995). Moth groups that are sensitive to floristic change and which have low vagility, such as the Geometridae and some Pyralidae, fulfil these criteria and have been demonstrated to be good indicators across a variety of ecological investigations (Beck *et al.* 2002; Holloway 1985; Kitching *et al.* 2000; Scoble 1995).

The set of moth species identified will be usefully incorporated as part of a 'predictor set' of arthropod and plant species, reflecting different trophic levels and guilds within the rainforest community. This will be significant for the ecological monitoring of future changes in ecosystem composition and function (Kitching 1993; McGeogh 1998).

The generality of our results is inevitably a potential point of contention. Firstly, we have examined only a single gradient within a single biome and a single catchment at one latitude. Although it is likely, as a general principal, that the higher taxa we have identified are likely to be useful generators of indicator species at other rainforest locations, no claims for generality of our results beyond the target locations can be (or is) made. Wider distribution records (as well as altitudinal information) for the indicator species are being collected from the Australian National Insect Collection, Canberra, and other museums. Future research will target additional rainforest transects within Australia at a range of scales. In particular, the local role of aspect and the continental role of latitude require investigation. This work is in progress.

Clearly, because of the way sites are necessarily distributed across the altitudinal gradient, geographic distances between sites will be correlated with moth assemblages. It is impossible to separate how much of this correlation is driven by inter-site distances and how much by the effects of altitude *per se*. However, the most parsimonious and most ecologically sensible explanation is that moth assemblages are more highly influenced by altitude (and the suite of environmental variables that are associated with altitude). Further work at additional altitudinal gradients, such as at Border Ranges National Park, will help test this hypothesis.

The analyses we have presented here are the first, necessarily, preliminary results of the Lepidoptera studies within the IBISCA-Queensland project. Further analyses examining responses on a family by family basis, formal quantification of 'indicator values' (Dufrene & Legendre; 1997), and comparisons of the ground-zone catches with those from the canopy, will probably also be informative.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from

the Federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We thank IBISCA-Qld team and the volunteers who helped collect and sort moths in October 2006, March 2007 and January 2008 as part of the IBISCA Queensland project, particularly John Gray, Heather Christensen, Kyle Barton, Dean Wright, Cecilia Chavana-Bryant, Jake Bryant, Stefan Curtis, Kyran Staunton and Eileen Forster for their help in field and laboratory work. Thanks also to Aki Nakamura for his valuable guidance with statistical analyses and to Geoff Thompson for photographing and preparing the plate of moths. The Environmental Futures Centre at Griffith University, Queensland, provided financial support for this paper, for which we are most grateful. We thank the Queensland Museum for allowing access to their reference collections of moths. Many improvements have been made to this manuscript thanks to feedback from Jude Buckman, Bob Ashton and Kyran Staunton.

LITERATURE CITED

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Couson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8: 1-16.

Beccaloni, G.W. & Gaston, K.J. 1994. Predicting the species richness of Neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation* 71: 77-86.

Beck, J., & Chey, V.K. 2008. Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. *Journal of Biogeography* 9: 1-13.

Beck, J., Schulze, C.H., Linsenmair, K.E & Fiedler, K. 2002. From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology* 18: 33-51.

Boulter, S.L., Lambkin, C. & Starick, N. 2011. Assessing the abundance of seven major arthropod group along an altitudinal gradient in sub-tropical rainforest. *Memoirs of the Queensland Museum-Nature* 55(2): 303-313.

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349.

Brehm, G. 2007. Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland forest. *Basic and Applied Ecology* 8: 44-54.

Brehm, G. & Fiedler, K. 2003. Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography* 30: 431-440.

2004. Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. *Journal of Tropical Ecology* 20: 165-172.

Brown, K.S. & Freitas, A.V.L. 2000. Atlantic Forest Butterflies: indicators for landscape conservation. *Biotropica* 32: 934-956.

Clarke, K.R., Gorley, R.N. 2006. PRIMER v6: User Manual/Tutorial. (PRIMER-E: Plymouth).

Common, I.F.B. 1990. *Moths of Australia*. (University of Melbourne Press: Melbourne).

Dobzhansky, T. 1950. Mendelian populations and their evolution. *The American Naturalist* 84: 401-418.

Dufrene M. & Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345-366.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A, Karl, T.R. & Mearns, L.O. 2000. Climate extremes: observations, modelling, and impacts. *Science* 289: 2068-2074.

Ellis, C.J., Coppins, B.J., Dawson, T.P. & Seaward, R.D. 2007. Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation* 140: 217-235.

Fiedler, K. & Beck, E. 2008. Investigating gradients in ecosystem analysis. Pp. 49-54. *In*, Bendix, E.B.J., Kottke, I., Makeschin, F. & Mosandl, R. (eds) *Gradients in a tropical mountain ecosystem of Ecuador*. (Springer-Verlag: Berlin).

Fielder, K., Brehm, G., Hilt, N., Subenbach, D. & Hauser, C.L. 2008. Variation of diversity patterns across moth families along a tropical altitudinal gradient. Pp. 167-179. *In*, Beck, E. (ed) *Ecological Studies 198*. (Springer-Verlag: Berlin).

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55: 73-106.

Frost, S.W. 1957. The Pennsylvania insect light trap. *Journal of Economic Entomology* 50: 287-292.

Grabherr, G., Gottfried, M. & Pauli, H. 1994. Climate effects on mountain plants. *Nature* 369: 448–488.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Review* 80: 489-513.

Holloway, J.D. 1985. Moths as indicator organisms for categorising rain-forest and monitoring changes and regeneration processes. Pp. 235-242. *In*, Chadwick, A.C. & Sutton, S.L. (eds) *Tropical Rain Forest: The Leeds Symposium*. (Leeds Philosophical and Literary Society: Leeds).

1998. The impact of traditional and modern cultivation practices, including forestry, on Lepidoptera diversity in Malaysia and Indonesia. Pp. 567-597. *In*, Newbery, D.M. (ed) *Dynamics of Tropical Communities*. (Cambridge University Press: Cambridge).

Holloway, J.D., Kirk-Spriggs, A.H. & Khen, C.V. 1992. The response of some rainforest insect groups to logging and conversion to plantation. *Philosophical Transactions: Biological Sciences* 335: 425-436.

Hutchinson, E.H. 1957. Concluding remarks. *Cold Spring Harbor symposium on quantitative biology* 22: 415-425.

IPCC. 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* (Cambridge University Press: Cambridge).

Kitching, R.L. 1993. Rainforest canopy arthropods: problems for biodiversity assessment. Pp. 26-30. *In, Rapid Biodiversity Assessment, Proceedings of a Workshop.* (Unit for Biodiversity and Bioresources: Macquarie University).

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology* 37: 284-297.

Kitching, R.L., Boulter, S.L., Vickerman, G., Laidlaw, M., Hurley, K.L. & Grimbacher, P.L. 2005. *The Comparative Assessment of Arthropod and Tree Biodiversity in Old-World Rainforests: The Rainforest CRC/Earthwatch Protocol Manual*, 2nd edition revised. (Rainforest CRC: Cairns).

Kitching, R.L, Putland, D.A., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum–Nature* 55(2): 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum–Nature* 55(2): 271-290.

Loope, L.L. & Giambelluca, T.W. 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. *Climatic Change* 39: 503-517.

McCoy, E.D. 1990. The distribution of insects along elevational gradients. *Oikos* 58: 313-322.

McDonald, W.J.F. & Hunter, J. 2010. The vegetation. *In*, (Kitching, R.L., Braithwaite, W. & Cananagh, J. (eds) *Remnants of Goudwana.* (Surrey Beatty: Sydney).

Malhi, Y. & Phillips, O.L. 2004. Tropical forests and global atmospheric change: a synthesis. *Philosophical Transactions of the Royal Society of London* 359: 549-555.

McGeogh, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73: 181-201.

Muirhead-Thomsom, R.C. 1991. *Trap responses of flying insects. The influence of trap design on capture efficiency.* (Academic Press Limited: London).

Nadkarni, N.M. & Solano, R. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. *Oecologia* 131: 580-586.

New, T.R. 1997. Are Lepidoptera an effective 'umbrella group' for biodiversity conservation? *Journal of Insect Conservation* 1: 5-12.

Nowinszky, L. 2004. Nocturnal illumination and night flying insects. *Applied Ecology and Environmental Research* 2:17-52.

Parmesan, C. 1996. Climate change and species' range. *Nature* 382: 765-766.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Pounds, J.A., Fogden, M.P. & Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611-615.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology* 15: 378-388.

Schulze, C.H., Linsenmair, K.E. & Fielder, K. 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology* 153: 133-152.

Scoble, M.J. 1995. *The Lepidoptera*. (The Natural History Museum and Oxford University Press: Oxford).

Shoo, L.P., Williams, S.E. & Hero, J.-M. 2006. Detecting climate change induced range shifts: where and how should we be looking? *Austral Ecology* 31: 22-29.

Stevens, N.C. 1997. Geology and landforms. Pp. 1-6. *In*, Monroe, R. & Stevens, N.C. (eds) *The Border Ranges: a Land Use Conflict in Regional Perspective* (Royal Society of Queensland: Brisbane).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum–Nature* 55(2): 251-270.

Still, C.J., Foster, P.N. & Schneider, S.H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608-611.

Suttle, K.B., Thomsen, M.A. & Power, M.E. 2007. Species interactions reverse grassland responses to climate change. *Nature* 315: 640-642.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Siqueira, M.F. de, Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Miles, G.F.M., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. 2004. Extinction risk due to climate change. *Nature* 427: 145-148.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-150.

Webb, L.J., & Tracey, J.G. 1978. A general classification of Australian rainforests. *Australian Plants* 9: 349-363.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.A.D., Smith, S.D., Tissue, D.T., Zak, J.C. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53: 941-952.

Williams, S.E., Bolitho, E.E. & Fox, S. 2003. Climate change in Australian tropical rainforest: an impending environmental catastrophe. *Proceedings of the Royal Society of London* 270: 1887-1892.

Willmont, W. 2004. *Rocks and Landscapes of the National Parks of Southern Queensland*. (Geological Society of Australia: Brisbane).

Yela, J.L. & Holyoak, M. 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Entomological Society of America* 26:1283-1290.

Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia

Chris J. BURWELL

Akihiro NAKAMURA

Biodiversity Program, Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia.

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia.

Citation: Burwell, C.J. & Nakamura, A. 2011 12 20: Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum — Nature* 55(2): 391-411. Brisbane. ISSN 0079-8835.

ABSTRACT

We present the distributions of ant species along an altitudinal gradient from 300 to 1100 m above sea level (m a.s.l.) within continuous rainforest in subtropical Queensland, Australia. Ants were collected along a single transect from four replicate plots at each of five zones of elevation (300, 500, 700, 900 and 1100 m a.s.l.) using a large array of methods targeting a wide range of microhabitats. These samples yielded a total of 170 ant species, represented by workers or ergatoid queens. A systematic ant sampling protocol, incorporating leaf litter extracts, spraying tree trunks with insecticide and hand collecting, was systematically conducted across all replicate plots in three seasons (spring, summer and autumn) enabling rigorous analysis of altitudinal patterns of species richness and assemblage structure. Species richness progressively declined with increasing altitude, with significant differences in the number of ant species between all zones except 300 and 500 m. Ant assemblages were significantly different among altitudinal zones with a progressive change in structure with increasing altitude between 300 and 900 m. Ant assemblages at 1100 m were markedly different to those at 900 m largely due to a dramatic decline in species richness rather than altitudinally restricted species. Short-term climate warming, therefore, may be of minor direct conservation concern for ants at this location. However, given the clear altitudinal signal of ant assemblages demonstrated here, ants have great potential as indicators of climate change-induced altitudinal range shifts. ❐ *ant species, Lamington National Park, IBISCA.*

Altitudinal stratification of assemblage structure is a generally accepted phenomenon for many invertebrate groups including moths (e.g. Brehm & Fiedler 2003; Brehm *et al.* 2007), butterflies (Fleishman *et al.* 2000; Wilson *et al.* 2007b), beetles (Monteith & Davies 1991; Escobar *et al.* 2005), flies (Wilson *et al.* 2007a), spiders (Monteith & Davies 1991; Chatzaki *et al.* 2005) and ants (Fisher 1999; Sanders *et al.* 2007). Many species of invertebrates are restricted to certain altitudinal ranges (Pyrcz & Wojtusiak 2002; Chatzaki *et al.* 2005; Botes *et al.* 2006), and some are only found at the upper limits of altitudinal gradients (Wilson *et al.* 2007a). These restricted altitudinal ranges have strong implications for assessing the impacts of climate change as upward shifts in distribution or complete disappearance of certain species at

higher altitudes are predicted to occur with increasing temperatures (Hodkinson 2005; Sanders *et al.* 2007).

In order to document differential responses of invertebrates to climatic changes, we need to establish baseline data describing the current altitudinal distributions of a wide range of invertebrate groups that may exhibit different ecological, evolutionary and physiological traits (Lomolino 2001; Calosi *et al.* 2008; Merrill *et al.* 2008). The IBISCA Queensland project was designed to document the current distributions of a range of invertebrate taxa along an altitudinal gradient within continuous rainforest in south-east Queensland. Specifically, the project aimed to identify taxa or suites of taxa that could be incorporated into long-term monitoring programs to detect the impacts of climate change. Here, we report on the altitudinal distribution of ants along the IBISCA transect.

Ant assemblages are known to be strongly stratified by altitude within a variety of vegetation and climatic zones, in both the northern and southern hemispheres (e.g. Fisher 1996; Samson *et al.* 1997; Bruhl *et al.* 1999; Sanders *et al.* 2003; Lessard *et al.* 2007). However, altitudinal studies of ants have largely focussed on the ground fauna, using pitfall trapping, litter extraction or a combination of both (e.g. Fisher 1999; Robertson 2002; Botes *et al.* 2006; Sanders *et al.* 2007). In contrast, we conducted specialist ant sampling which incorporated three methods (leaf litter extracts, spraying tree trunks with insecticide and hand collecting). This suite of methods targeted both ground and arboreal ants, as well as specialist nesters within and under rotting logs and rocks. Data from this systematic protocol were supplemented from ants collected using a large number of other methods employed during the IBISCA project.

The aims of the present study are broadly threefold. First, we establish an inventory of ant species along the altitudinal gradient of rainforest at Lamington National Park, using available data from all collecting methods used during the IBISCA project. This provides the most comprehensive baseline information on the altitudinal distribution of ant species within the region, where almost no ecological studies of ants have been previously conducted (but see Majer *et al.*, 2001). Secondly, we assess the effectiveness of our systematic protocol in sampling the ant fauna along the gradient. Thirdly, we analyse altitudinal patterns of ant species richness and assemblage structure to examine the utility of ants as bio-indicators of future climate change.

MATERIALS AND METHODS

Study site and design

The study site is a single altitudinal transect in the Green Mountains Section of Lamington National Park in the south-east corner of Queensland, Australia. The transect lies in continuous rainforest within the West Canungra Creek catchment. Climatic conditions vary along the transect, but at the Green Mountains National Park headquarters (approximately 940 m.a.s.l.) annual rainfall averages 1827 mm with most falling in summer. Average air temperatures range from a 4°C minimum in winter to 27°C maximum in summer. (see Kitching *et al.* 2011 for a detailed description of the transect).

Four experimental plots (A-D) were established at each of five zones of elevation; 300, 500, 700, 900 and 1100 m.a.s.l. (20 plots in total, see Kitching *et al.* 2011 for precise coordinates and elevations). Within each zone, plots were separated by at least 400 m. Forest structure and species composition varied along the transect (see Laidlaw *et al.* 2011). The low elevation plots (300 m a.s.l.) are located within *Araucaria* complex notophyll vine forest , the mid elevation plots (500-900 m a.s.l.) within complex notophyll vine forest and the 1100 m plots within simple microphyll fern forest dominated by Antarctic Beech, *Nothofagus moorei*. All plots had basaltic

soils derived from Cainozoic rocks. Each plot consisted of a central 20 m × 20 m quadrat and a surrounding circular survey area of 50 m radius measured from a metal stake located in the centre of the quadrat (see Kitching *et al.* 2011 for a detailed description of the experimental design).

SYSTEMATIC SAMPLING

Systematic sampling was designed to provide a robust measure of the overall ant fauna within a plot and was intended as a standard protocol that could be used for future monitoring of the impacts of climate change. Three systematic sampling methods targeted different elements of the ant fauna. Tullgren funnels (litter extracts) sampled the leaf litter fauna, spraying tree trunks with synthetic pyrethroid insecticide (bark sprays) sampled the arboreal fauna and timed bouts of hand collecting during the day (day hand) provided a general overview of the ant fauna while also sampling large species and specialist nesters rarely collected by the two previous methods. Systematic sampling involved the collection of one day hand sample, two litter extracts and two bark spray samples per plot in each sampling period. Systematic sampling was conducted at all elevations and plots in three periods each representing a different season: 16-27 October 2006 (spring), 8-20 March 2007 (autumn) and 17-29 January 2008 (summer). In summer 2008, bark sprays were conducted at two 1100 m plots on February 10 due to wet conditions during January.

Litter extracts

The two litter extracts per plot per season were collected from outside the central quadrat at opposite sides of the plot. Each extract was derived from 1 m^2 of leaf litter collected as four 50 cm × 50 cm squares at least 5 m distant from each other. Squares were not chosen randomly but consisted of areas with relatively uniform litter coverage. Thick rain-washed deposits of litter and soil were avoided. All litter and loose surface soil within the four squares was collected by hand, sieved with a litter sifter with a hexagonal mesh of chicken wire of approximately 15 mm in diameter. Litter extracts were transferred to a cloth bag and processed in Tullgren funnels within 24 hours of collection. Funnels were usually operated for 24 hours with a single 60 watt incandescent bulb, but wetter extracts were processed for up to 36 hours.

Bark sprays

Two bark spray samples were collected per plot per season from opposite sides of the plot. For each sample, five trees located outside the central quadrat were selected. Large trees (> 30 cm diameter at breast height (dbh)) were targeted, especially those encrusted with vines, epiphytes or moss. Their trunks were thoroughly sprayed using hand-held cans of pyrethroid insecticide (Mortein Fast Knockdown®), insecticide and the jet directed from the base to as far as possible up the trunk. Falling insects were collected on a rectangular sheet of rip-stop nylon (160 cm × 105 cm) placed at the base of each tree. Approximately 15 minutes after spraying, the five sheets were collected and their catches transferred to an ethanol filled vial using a suspended fabric funnel.

Day Hand Collecting

A single day hand sample was collected per plot per season. Ants were collected for 60 minutes by C.J. Burwell (CJB) within the 50 m radius of the plot, including the central quadrat. Day hand samples were collected between 0905 and 1650 hrs. Foraging workers on the ground, logs, foliage and tree trunks were collected. In addition, ant nests were searched for under rocks, within and under fallen logs and epiphytes and inside hollow branches and twigs. Not all observed worker ants were collected, rather the aim was to maximise the number of species collected.

TABLE 1. Summary of collection methods yielding supplementary ant samples examined in this study. See Ødegaard & Diserud (2011) for more detailed description of the beating and sampling methodology.

Method	Brief description of sampling methodology	Sampling period						Samples examined
		Oct.06	Jan.07	Feb.07	Mar.07	Jul.07	Jan.08	
Night hand	Each sample was a 30 min. bout of hand collecting at night (between 1830 and 2240 hrs), searching for active workers (not nests). Two or three samples collected per plot.	*			*		*	Oct & Mar: 300A, C; 500A-B; 700A-B; 1100C-D (no 500's in Oct). Jan.: 700A-D; 900A-D.
Malaise traps	One Townes Malaise trap per plot operated for 10 days.	*	*		*	*		All plots
Pitfalls	9 mm x 42 mm internal diameter cylindrical pitfall traps per plot, arrayed in a cross; open for 9 days; filled with 70% ethanol (Oct., Feb., Mar.) or propylene glycol (Jan.); 9 individual trap catches pooled into one sample.	*	*	*	*			All plots Jan. 300D sample lost.
Baited pitfalls	4 rectangular pitfall traps (125 mm x 87 mm) per plot, situated 25 m from central stake along main compass points; open for 10 days, each baited with wallaby dung (5 days) and mushrooms (5 days); catches from 4 traps pooled into one sample.	*	*			*		All plots
FIT – Flight intercept traps	One FIT per plot, operated for 10 days; each trap consisted of a vertical rectangular panel (66 cm x 70 cm) of layers of plastic kitchen wrap above a rectangular collecting container (14 cm x 66 cm) raised above ground level and filled with propylene glycol.	*	*		*			All plots
Yellow pans	Three yellow pans (rectangular plastic food containers approx. 165 mm x 110 mm) placed on ground within the central square, operated for three days per plot; catches from 3 traps pooled into one sample.	*			*			All plots
Baseline litter extracts	1 litre of unsifted leaf litter was collected from a single location within the central quadrat of each plot and extracted with a Tullgren funnel for 6 days.	*	*		*			All plots
Baseline bark sprays	1 m x 1 m squares of bark, at breast height, of living tree trunks within central quadrat were sprayed with synthetic pyrethroid insecticide and falling invertebrates collected on plastic sheets; 3-6 trees per plot were sprayed and their catches pooled into one sample.	*						300A-C; 500A, C; 700A-B; 900B-C; 1100A-C
Sweeping	15 minutes of sweeping low vegetation (40 cm internal diameter hoop size) per plot.	*			*			All plots
Beating	For each sample all vegetation (alive and dead) along a 20 m transect was beaten with a 1.5 m long stick and a 1 m x 1 m nylon beating sheet.	*						Miscellaneous samples from 300B-D; 700C; 900B-C.
Tuna baits	25 tuna baits each placed on the ground and on foliage within central quadrat of each plot; ants collected after 30 minutes; ants from all 50 baits pooled into one sample	*						All plots except 700C and 700D

Supplementary sampling

All other samples (i.e. those not systematically collected or not specifically targeting ants) containing ants were deemed supplementary samples, and were used to augment species richness and give a more comprehensive inventory for each plot. The samples included a small number of extra litter extracts, bark sprays and day hand samples collected in spring, summer and autumn, and a comprehensive set of litter extracts and bark sprays collected from all plots in winter 2007 (22-27 July). Additional supplementary samples were obtained from numerous other collection methods employed across a variety of plots and seasons (summarised in Table 1). The sampling effort employed at each plot and

TABLE 2. Summary of sampling 'intensity' (systematic and supplementary) across the five elevations (see Table 1 and text for definition of a sample for each collection method). Number of samples collected on the left of each cell; samples containing ants in parentheses. Total abundance (workers and ergatoid queens) for quantitative methods, total incidences (the occurrence of species within samples) and total species collected are collated for each method. *Beating was systematically undertaken across all elevations and plots, but only a small fraction of ants from beating samples were available for study.

Sampling method	Altitudinal Zone					Total abuncance	No. Incidences	No. species
	300 m	500 m	700 m	900 m	1100 m			
Systematic samples								
Litter extract	24 (24)	24 (24)	24 (24)	24 (24)	24 (22)	10297	942	78
Day hand	12 (12)	12 (12)	12 (12)	12 (12)	12 (12)	na†	834	100
Bark spray	24 (24)	24 (24)	24 (24)	24 (24)	24 (24)	3708	704	87
Supplementary samples								
Pitfall	15 (15)	16 (16)	16 (16)	16 (16)	16 (11)	4106	611	75
Night hand	10 (10)	4 (4)	21 (21)	25 (25)	8 (8)	na†	420	59
Baited pitfall	12 (12)	12 (12)	12 (11)	12 (12)	12 (11)	1795	385	83
Litter extract (non-systematic)	10 (10)	8 (8)	10 (10)	11 (11)	8 (8)	1450	238	48
Malaise	12 (12)	12 (10)	12 (12)	12 (10)	12 (6)	796	238	54
FIT	12 (12)	12 (10)	12 (11)	12 (11)	12 (6)	293	164	60
Baseline berlesate	12 (11)	12 (10)	12 (10)	12 (11)	12 (5)	362	119	32
Tuna baits	4 (4)	4 (4)	2 (2)	4 (4)	4 (3)	na†	108	33
Bark spray (non-systematic)	9 (8)	8 (7)	8 (7)	8 (6)	10 (6)	301	74	25
Sweeping	8 (5)	8 (6)	8 (7)	8 (4)	8 (1)	71	48	19
Baseline pyrethrum	3 (2)	2 (2)	2 (2)	2 (2)	3 (2)	279	47	26
Yellow pan	8 (7)	8 (6)	8 (7)	8 (5)	8 (2)	64	42	28
Day hand (non-systematic)	2 (2)	0	0	1 (1)	3 (3)	na†	35	26
Beating*	3 (3)	0	1 (1)	2 (2)	0	46	18	12
TOTAL samples	180 (174)	166 (155)	184 (177)	193 (180)	176 (130)			170

† Only incidences (not abundances) of species were recorded from samples collected with these methods and total ant abundances are not applicable (na).

the number of samples that yielded ants are summarised in Table 2.

Sorting and identification

This study is based on the occurrence of wingless workers and/or ergatoid queens of species within samples, as their presence is a reliable indication that those species are nesting within the plots. Winged or dealate reproductives however, may have dispersed from outside the confines of the plot. In addition, reproductives, especially males, could not always reliably be associated with their respective workers. Consequently, winged and delate reproductives have generally been ignored in this study, apart from six species for which they were the only castes collected.

Workers and ergatoid queens from all available IBISCA samples were processed and identified to morphospecies. Where possible, they were identified as described species using the published taxonomic literature, by comparison with type and critically identified specimens in the Australian National Insect Collection, or through the advice of, specialist taxonomists (Monomorium, Brian Heterick; Polyrhachis, Rudy Kohout). Unidentified taxa were assigned species codes that are specific to this project. A voucher collection of more than 3000 pinned ants, representing all species collected during the survey, is housed at the Queensland Museum. The generic classification used here follows Shattuck & Barnett (2001) and the subfamily classification follows Bolton (2003).

Data analysis

Ant assemblages were analysed as two datasets: ants from all samples (i.e. systematic and supplementary samples combined; for descriptive analyses only) and those from systematic samples alone (which allowed for fully balanced statistical analyses). Before analysis, ants collected from different sampling methods were pooled and their abundances were transformed to incidence (presence or absence) because some of the sampling methods (e.g. day and night hand collecting) only recorded the presence of species in samples. The unit of replication is a plot within each altitudinal zone (n=4), except for rarefaction curves where seasonal samples were treated separately to assess sampling sufficiency (n=12).

We first tested the sampling sufficiency of the systematic ant collecting protocol by generating sample-based rarefaction curves using the expected richness function (MaoTau) with EstimateS software ver. 8.0.0 (Colwell 2004). Sample-based rarefaction curves represent expected species richness, given n samples (n=12) for each altitudinal zone. The asymptote of each rarefaction curve was estimated with EstimateS using the Michaelis-Menten richness estimator (MM-Means). The shape of the rarefaction curve and the discrepancy between observed species richness and values of MM-Mean were used to evaluate sampling sufficiency at each altitudinal zone. Species richness of the local ant community within each altitudinal zone was estimated using the incidence-based coverage estimator (ICE). To test for differences in species richness among different altitudinal zones, single-factor ANOVA was performed with SPSS rel. 13.0 (SPSS Inc. 2004). For post-hoc pairwise comparisons we employed LSD tests. Inflation of type I error was not controlled as the risk of Type II error was high due to the small sample size at each altitudinal zone (n=4).

We used PRIMER ver. 5 (Clarke, 1993) to generate non-metric multi-scaling (NMDS) ordinations based on Sorensen similarity matrices calculated between each site pair, with 10 random restarts. NMDS ordinations were generated based on all samples (systematic plus supplementary) and systematic samples alone. The similarity between the two ordinations was compared using Mantel-type Spearman rank correlation on the similarity matrices (RELATE

TABLE 3. Generic distribution of 176 ant species recorded from the entire altitudinal transect. Species represented only by winged or dealate reproductives in parentheses. Genera marked with an asterisk contain at least one species considered to be characteristic of open forest, or likely to have been introduced to the plots via contamination of samples.

Genus	# spp.
MYRMECIINAE	
Myrmecia	2
CERAPACHYINAE	
Cerapachys	6
Sphinctomyrmex	2
AMBLYOPONINAE	
Amblyopone	2 (2)
Onychomyrmex	1
Prionopelta	1
HETEROPONERINAE	
Heteroponera	2
PONERINAE	
Cryptopone	2
Hypoponera	7
Leptogenys	5
Myopias	1 (1)
Pachycondyla	4
Platythyrea	1
Ponera	1
PROCERATIINAE	
Discothyrea	4
Probolomyrmex	1
ECTATOMMINAE	
Rhytidoponera	3
MYRMICINAE	
Anisopheidole	1
Cardiocondyla	(1)
Carebara	2
Colobostruma	4
Crematogaster	4
Eurhopalothrix	1
Lordomyrma	2
Machomyrma	1
Mayriella	3
Metapone	(2)
Monomorium	9
Myrmecina	1
Orectognathus	7
*Pheidole**	12
Podomyrma	9
Pristomyrmex	2
Rhopalomastix	1
Rhopalothrix	1
Solenopsis	1
Strumigenys	5
*Tetramorium**	1
FORMICINAE	
Acropyga	1
Camponotus	6
Myrmecorhynchus	2
Notoncus	2
Notostigma	1
Nylanderia	1
Paraparatrechina	3
*Paratrechina**	1
*Plagiolepis**	2
*Polyrhachis**	8
Prolasius	7
Stigmacros	4
Teratomyrmex	1
DOLICHODERINAE	
Anonychomyrma	2
Bothriomyrmex	1
*Iridomyrmex**	3
*Leptomyrmex**	4
*Ochetellus**	3
Tapinoma	4
*Technomyrmex**	2
Total genera	58
Total species	176

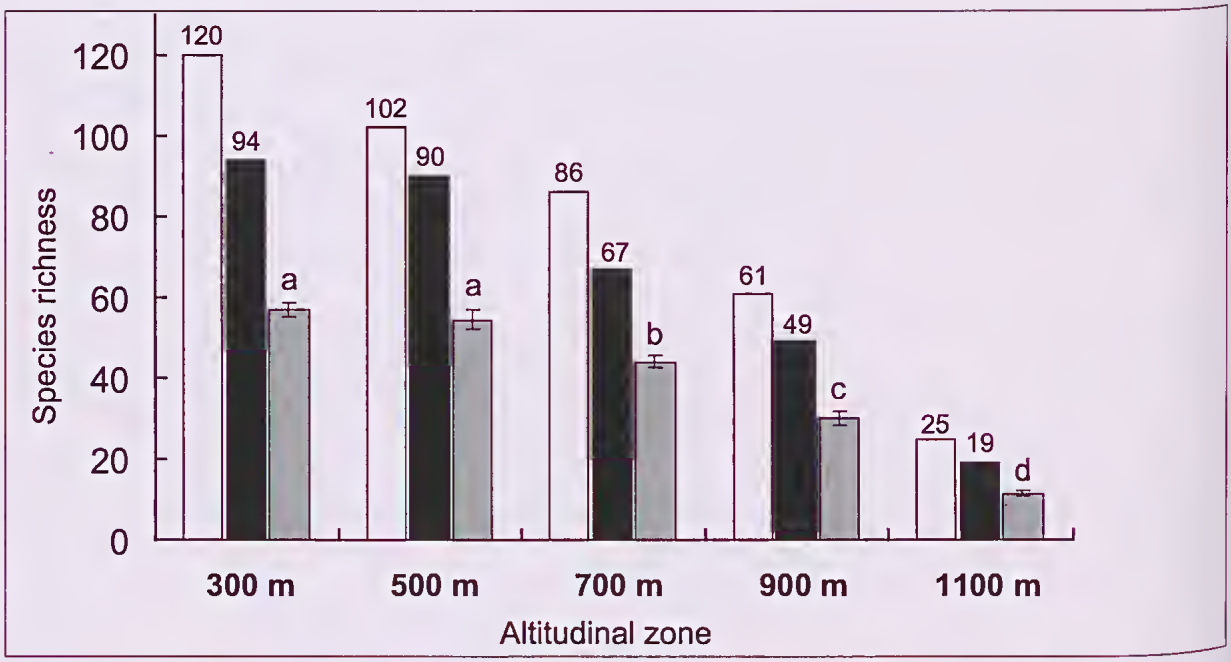


FIG. 1. Total species richness based on all samples (white bars) and systematic samples (black bars) with actual number of species shown above the bars. Mean species richness (with standard errors) based on systematic samples also shown with grey bars. Results of post-hoc LSD tests are shown with different letters indicating significant differences between altitudinal zones.

function in PRIMER), with 999 permutations. Non-metric multivariate ANOVA was performed with PERMANOVA software to test for differences in ant assemblage composition among altitudinal zones. This software executes multivariate ANOVA, using permutation methods, to calculate *P* values derived from pseudo *F* statistics of the distance measures (Anderson 2005). For each post-hoc pairwise test, PERMANOVA calculates the multivariate version of the *t*-statistic and Monte Carlo asymptotic *P* values which are not restricted by the number of unique permutations. Multivariate analyses were only carried out for systematic

TABLE 4. Numbers of shared species between altitudinal zones (above the diagonal) and unique species to each altitudinal zone (in the diagonal shown in bold), based on ant assemblages collected by all sampling methods. Numbers of shared and unique ant species derived from systematic sampling methods are shown in parentheses. Values below the diagonal are *t*-statistics calculated from post-hoc Monte Carlo permutation tests of PERMANOVA based on ant assemblages collected by systematic samples only. Larger values of *t*-statistic indicate greater dissimilarities in ant assemblage composition between altitudinal zones.

	300 m	500 m	700 m	900 m	1100 m
300 m	**41 (29)**	73 (60)	56 (41)	38 (30)	11 (5)
500 m	2.12	**7 (9)**	72 (56)	44 (36)	16 (13)
700 m	3.75	2.21	**6 (5)**	46 (35)	16 (12)
900 m	3.97	3.05	2.41	**5 (6)**	19 (12)
1100 m	5.92	5.09	5.51	4.01	**1 (4)**

All *t*-statistics are significant at $P<0.01$, except between 300 and 500 m where $P<0.05$.

TABLE 5. Comparison of the number of ant species (richness) collected at each study plot using both supplementory and systematic sampling methods (total) and systematic sampling methods only, with systematic richness expressed as a percentage of the total richness. Effectiveness of the systematic sampling methods averaged across the four plots within each altitudinal zone.

Elevation & Plot	Total richness	Systematic richness	% systematic vs total	Mean % (±SD) systematic vs total
300A	85	57	67.06	73.82 ± 4.67
300B	79	60	75.95	
300C	76	59	77.63	
300D	71	53	74.65	
500A	70	51	73.17	78.68 ± 4.89
500B	63	50	73.75	
500C	72	56	73.96	
500D	72	60	81.25	
700A	58	46	79.31	76.48 ± 4.40
700B	59	47	79.66	
700C	57	40	70.18	
700D	56	43	76.79	
900A	45	28	62.22	76.24 ± 9.77
900B	38	32	84.21	
900C	32	26	81.25	
900D	44	34	77.27	
1100A	14	10	71.43	73.17 ± 6.07
1100B	15	11	73.33	
1100C	18	12	66.67	
1100D	16	13	81.25	

samples as the dataset consisting of all samples suffers from seasonal and altitudinal sampling bias (see Tables 1 & 2).

RESULTS

Overall ant assemblage composition

A total of 170 ant species from 56 genera, represented by workers or ergatoid queens, were collected across the transect using all sampling methods (Table 3). An additional six species were represented only by winged or dealate reproductives. The altitudinal distributions of all species and their occurrence at the replicate plots within each elevational zone are summarised in Appendix 1. The majority of recorded species are known inhabitants of rainforest. However, a few species that were rarely collected (*Iridomyrmex* spp., *Ochetellus* spp., *Polyrhachis ornata*, *Plagiolepis* IBISCA2, *Leptomyrmex rufipes*) are likely to be transients from nearby open forest and a few species

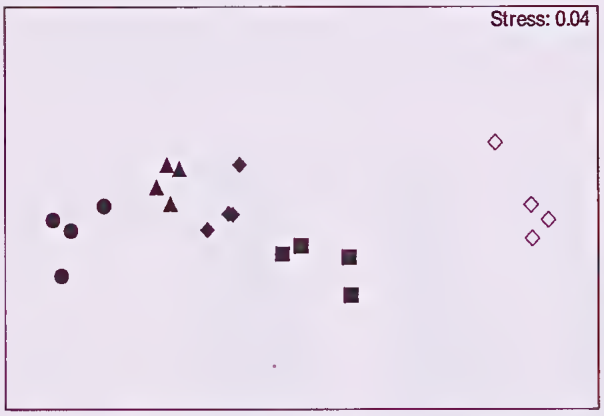


FIG. 2. NMDS ordinations based on ant assemblages collected from both systematic and supplementary samples (●, 300 m; ▲, 500 m; ◆, 700 m;■, 900 m; ◇, 1100 m). Ordinations were generated based on species' incidences (presence/absence) at a plot with data from all methods and seasons pooled.

associated with disturbed environments (*Pheidole megacephala*, *Pheidole* IBISCA8, *Tetramorium simillimum*, *Plagiolepis* IBISCA2, *Paratrechina longicornis*) were probably contaminants introduced with dung used in the baited pitfall trapping. However, the removal of these species from the overall dataset makes no appreciable differences in altitudinal patterns of species richness or assemblage structure and consequently they have not been excluded.

Using the complete dataset (all sampling methods combined) ant species richness peaked at the lowest elevation (300 m, 120 spp.) and progressively declined with increasing altitude (Fig. 1). Species richness was lowest at the highest elevation (1100 m, 25 spp.), dropping dramatically from that at 900 m (61 spp.). Ant assemblages were clearly correlated with altitude (Fig. 2). Replicate plots within each elevational zone formed distinct clusters on the NMDS ordination, with a progressive change in assemblages from the 300 to 900 m zones (Fig. 2). Paralleling the pattern for species richness, ant assemblages of the 1100 m plots were positioned along the altitudinal gradient, but were markedly separated from those of the 900 m plots (Fig. 2).

A total of 60 ant species were restricted to a single altitudinal zone, although more than half of these (31 spp.) were collected from single samples (effectively singletons). The 300 m zone had by far the most unique species, 41 including 20 'singletons'. All other zones had 7 or fewer unique species (Table 4) with only a single species (which was collected only once) unique to the 1100 m zone. The largest numbers of shared species were found between the 300 and 500 m (73) and 500 and 700 m (72) zones, while the least number of species was shared between 300 and 1100 m (11).

Ant assemblages from systematic sampling protocol

The systematic sampling protocol yielded a total of 143 ant species (represented by workers or ergatoid queens) across the entire transect, 84% of the 170 species represented by the complete dataset. At the level of the elevational zone, the systematic sampling methodology yielded between 76% and 88% of the complete inventory of species derived from all collecting methods. At the plot level, systematic samples yielded from 62% to 81% of the total species inventory (Table 5). However, when these values were averaged across the four plots within each altitudinal zone, the systematic sampling protocol yielded a remarkably consistent mean percentage of the plot species inventory (73-79%, Table 5).

For altitudinal zones at or above 700 m, rarefaction curves based on systematic samples (n=12) started to plateau (Fig. 3). Values of MM-Means were within the upper limit of 95% confidence intervals of accumulated species richness at the maximum number of samples, suggesting that the majority of species were collected from the plots within these altitudinal zones. For the 300 and 500 m altitudinal zones,

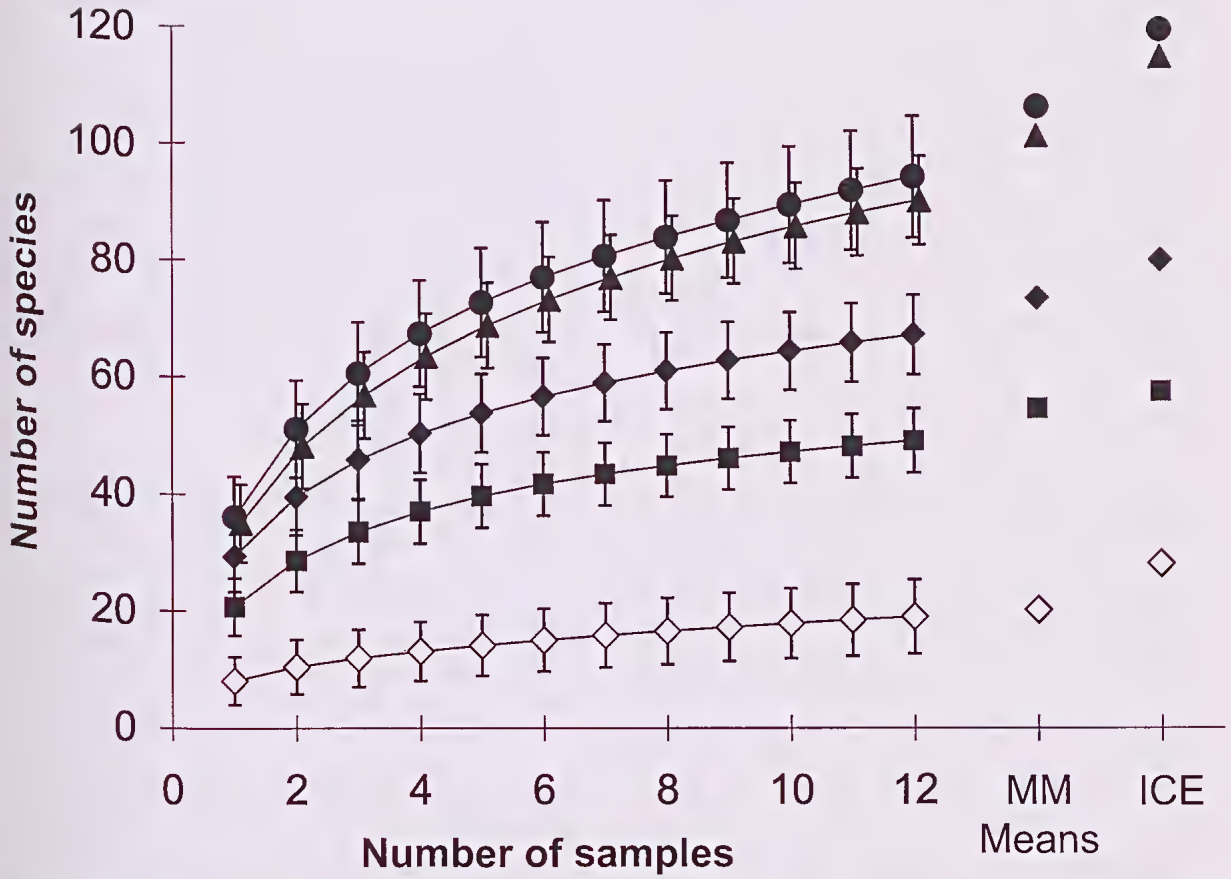


FIG. 3. Ant species rarefaction curves based on systematic samples. Rarefaction curves were generated for each altitudinal zone with 95% confidence intervals. (●, 300 m; ▲ 500 m; ◆ 700 m; ■, 900 m; ◇, 1100 m). Estimated species richness was also calculated using the asymptotic estimator (MM-Means) and the incidence-based coverage estimator (ICE) (see text for more details).

however, the terminal slopes of the rarefaction curves were noticeably steeper, with the values of MM-Means falling above the 95% confidence intervals. ICE predicted that the species richness of local ant communities would peak at 300 m altitudinal zone with 119 species, and would progressively decline with increasing altitude (115, 80, 57 and 28 species at 500, 700, 900, 1100 m respectively). These estimated species richness values were in broad agreement with the observed richness values based on all sampling methods, which yielded 120, 102, 86, 61 and 25 species at 300, 500, 700, 900, 1100 m respectively (Fig. 1). Species richness was significantly different among the altitudinal zones (ANOVA F=112.56, P<0.001) and post-hoc LSD tests indicated that species richness declined significantly from high to low altitudinal zones with the exception of 300 and 500 m, where no significant difference was found (Fig. 1).

The NMDS ordination based on systematic samples showed similar patterns to that based

on all samples (Mantel-type Spearman rank correlation: *Rho*=0.46, *P*<0.01. Ant assemblage compositions were significantly different between pseudo and F among altitudinal zones (PERMANOVA pseudo *F*=15.91, *P*<0.001) and post-hoc tests showed significant differences in all pairwise comparisons between zones (see also Table 5). The smallest differences in ant assemblage composition were found between 300 and 500 m (t = 2.117) and between 500 and 700 m (t = 2.207), and the greatest between 300 and 1100 m (t = 5.924).

DISCUSSION

This is the first study describing the altitudinal stratification of ants in Australia. In addition, it employs an extensive array of collecting methods targeting a very broad range of microhabitats. Despite the non-systematic nature of some sampling methods contributing to the complete dataset, the full inventory provides the most comprehensive information available on the distributions of ant species within rainforest along the altitudinal gradient. The significance of the complete inventory is reinforced by the generally consistent relationship between the observed total species richness (from systematic and supplementary samples) and values of ICE (estimated species richness derived from systematic samples) within elevations. The exception to this pattern was the 500 m zone where the observed species richness (102 spp.) was substantially lower than the estimated value (115 spp.), due perhaps to the lower number of samples (especially those from night hand collecting) taken there (Table 5).

Inevitably, our sampling protocols did not cover an exhaustive range of microhabitats. In particular, we may have missed species restricted to the upper canopy and perhaps those associated with tree hollows or the suspended soil of epiphytes. However, at least some of our methods, particularly bark spraying, Malaise traps and sweeping, probably collected canopy species foraging lower in trees. In addition, Majer *et al.* (2001) using canopy fogging within rainforest in the same study area, reported only 10-13 species of ants in two 10 × 10 m plots. In addition, we did not include methods to sample ants from deep within the soil. However, their inclusion is likely to have had little effect on observed patterns of assemblage structure as the fauna of strictly subterranean ants (e.g. Leptanillinae) probably consists of very few species.

Sampling sufficiency of the systematic protocol

Our systematic protocol sampled ants in a fully standardised manner from ground, arboreal and other specialised microhabitats, providing distributional data amenable to rigorous statistical analyses. However, compared to the complete dataset from all available samples, systematic samples underestimated the average species inventory per plot within each elevational zone by a substantial amount (21-27%). Despite these discrepancies in plot-based richness estimates, overall patterns of ant assemblage composition and richness across altitudinal zones were, nevertheless, consistent between systematic and complete datasets, suggesting the patterns found by the systematic sampling protocol are robust. We further scrutinised the sufficiency of systematic samples, using rarefaction techniques, to ensure that increased sampling intensity would not have changed the overall outcomes of the results. With respect to species richness, the shape of the rarefaction curves suggested potential undersampling at the lower altitudinal zones of 300 and 500 m.a.s.l. Increasing sampling intensity would have augmented species richness at these zones. However, values of the ICE and MM-means species richness estimators suggest that relative differences among altitudinal zones would likely be the same.

Species richness

We demonstrated that ant species richness was highest at low elevations and progressively declined above 500 m a.s.l. Similar monotonic declines in ant species richness with increasing altitude have been described for both tropical (Fisher 1996; Bruhl *et al.* 1999) and temperate regions (Lessard *et al.* 2007). However, more studies have found a mid-altitudinal peak in ant species richness with a subsequent decline at higher altitudes (Olson 1994; Samson *et al.* 1997; Fisher 1998; Fisher 1999; Sanders 2002; Sanders *et al.* 2003; Fisher 2004). Had we collected ants from even lower altitudes (i.e. 0-200 m) a mid-altitudinal peak may have emerged. However, we were unable to locate suitable sites as lowland rainforests have been extensively cleared, leaving only small rainforest remnants whose ant assemblages may not be directly comparable to that of continuous rainforest due to the effects of habitat fragmentation (Fahrig 2003).

Assemblage structure

Ant assemblage composition was significantly different among all altitudinal zones. On the NMDS ordinations, assemblage composition changed progressively with altitude, suggesting that neighbouring altitudes have more species in common than they have with other more distant altitudes. However, ant assemblages at the 1100 m plots were widely separated from those at 900 m, more than would be expected from an upslope shift of just 200 m. Ant assemblages at 1100 m were characterised by low species richness and almost no species occurred exclusively at this altitude. This dramatic change is perhaps related to the greater prevalence of cloud cover at the 1100 m plots. Vegetation communities also change dramatically from the 900 m plots (complex notophyll vine forest) to the 1100 m plots (simple microphyll fern forest). These marked changes in ant and vegetation communities may be related to increased levels of precipitation due to cloud-stripping at the highest elevations. Altitudinal studies in tropical rainforests outside Australia have also documented dramatic declines in the richness and abundance of ants at high elevations, associated with the transition into the zone of regular cloud formation (Samson *et. al.* 1997; Bruhl *et. al.* 1999). Many factors have been proposed to account for these observed declines, such as high humidity and soil moisture, low temperatures and solar radiation levels and a reduced leaf litter layer (Bruhl *et al.* 1999). Potential abiotic and biotic factors driving the structure of ant assemblages along this gradient will be the focus of future studies.

Faunal and floral assemblages occurring within the simple microphyll fern forest at the highest elevations at Lamington National Park are under most immediate threat due to climate warming. These areas are known to contain a number of altitudinally restricted and regionally endemic species, particularly invertebrates (Williams 2002). For example, Ødegaard and Diserud (2011), with respect to beetles, bugs and mutillid wasps associated with understorey vegetation, found that of the species unique to a single altitudinal zone, half were restricted to the 1100 m plots. In contrast, ant assemblages at 1100 m were characterised by low species richness and only a single species occurred exclusively at this altitude. Instead, most of the ant species unique to a particular altitudinal zone occurred at the lowest elevation, 300 m. Therefore, unlike many groups of invertebrates, the impacts of climate change may pose little conservation concern to ant species along the gradient in the short term.

Given the clear altitudinal signal of ant assemblages demonstrated here, it would appear that there is great potential to use ants to monitor altitudinal range shifts which may occur in response to increasing temperatures. Assemblage level responses to climate change have been demonstrated for butterflies in mountains in central Spain, where assemblages

with similar species composition have shifted uphill by approximately 300 m in around the last 30 years (Wilson *et al.* 2007b). The present study has established baseline data that will allow the detection of assemblage level responses of ants. Additionally, the replicated design of the IBISCA project can also enable rigorous statistical analyses to identify ant species that are indicative of particular altitudinal ranges. Monitoring of this suite of indicator species will facilitate the detection of differential species responses to climate change that may potentially obscure assemblage level responses.

ACKNOWLEDGEMENTS

Roger Kitching (Project leader), David Putland, Heather Christensen and all other IBISCA support staff and volunteers are thanked for their assistance during the project. Susan Wright, Geoff Thompson and Anna Marcora (Queensland Museum) are thanked for their huge efforts in conducting the systematic ant sampling. Other IBISCA participants, in particular, Geoff Monteith, Christine Lambkin, Kyran Staunton, Frode Ødegaard, Juergen Scmidl and Torsten Bitner provided access to the ants from their sampling programs. Finacial assistance was provided by a Queensland Government Smart State Grant, Griffith University, the Queensland Museum, Queensland Herbarium, SEQ Catchments Network and the Global Canopy Programme. Thanks also to Carla Catterall and other members of the WEDG discussion group for their helpful comments on the manuscript.

LITERATURE CITED

Anderson, M.J. 2005. PERMANOVA: a FORTRAN Computer Program for Permutational Multivariate Analysis of Variance. (Department of Statistics, University of Auckland: Auckland).

Bolton, B. 2003. Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute* **71**: 1-370.

Botes, A., Mcgeoch, M.A., Robertson, H.G., Niekerk, A., Davids, H.P. & Chown, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.

Brehm, G., Colwell, R.K. & Kluge, J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* **16**: 205-219.

Brehm, G. & Fiedler, K. 2003. Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography* **30**: 431-440.

Bruhl, C.A., Mohamed, V. & Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15**: 265-277.

Calosi, p., Bilton, d.T. & Spicer, j.I. 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology Letters* **4**: 99-102.

Chatzaki, M., Lymberakis, P., Markakis, G. & Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography* **32**: 813-831.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117-143.

Colwell, R.K. 2004. Estimates: Statistical Estimation of Species Richness and Shared Species from Samples. Version 7. User's Guide and Application. Published at: http://purl.oclc.org/estimates.

Escobar, F., Lobo, J.M. & Halffter, G. 2005. Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Global Ecology and Biogeography* **14**: 327-337.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**: 487-515.

Fisher, B.L. 1996. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andringitra, Madagascar. *Fieldiana Zoology* **85**: 93-108.

1998. Ant diversity patterns along an elevational gradient in the Reserve Speciale d'Anjanahanbe-Sud and on the Western Masoala Peninsula, Madagascar. *Fieldiana Zoology* **90**: 39-67.

1999. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale

d'Andohahela, Madagascar. *Fieldiana Zoology* **94**: 129-147.

2004. Diversity patterns of ants (Hymenoptera: Formicidae) along an elevational gradient on Monts Doudou in southwestern Gabon. *California Academy of Sciences Memoir* **28**: 269-286.

Fleishman, E., Fay, J.P. & Murphy, D.D. 2000. Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *Journal of Biogeography* **27**: 1209-1219.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**: 489-513.

Kitching, R.L., Putland, D.A., Ashton, L.A., Laidlaw, M.J., Boulter S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* 55(2): 235-250.

Lessard, J.P., Dunn, R.R., Parker, C.R. & Sanders, N.J. 2007. Rarity and diversity in forest ant assemblages of Great Smoky Mountains National Park. *Southeastern Naturalist* **6**: 215-228.

Lomolino, M.V. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**: 3-13.

Majer, J.D., Kitching, R.L., Heterick, B.E., Hurley, K. & Brennan, K.E.C. 2001. North-south patterns within arboreal ant assemblages from rain forests in eastern Australia. *Biotropica* **33**: 643-661.

Merrill, R.M., Gutierrez, D., Lewis, O.T., Gutierrez, J., Diez, S.B. & Wilson, R.J. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* **77**: 145-155.

Monteith, G.B. & Davies, V.T. 1991. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp. 345-362. In Werren, G. & Kershaw, P. (eds) *The Rainforest Legacy: Australian National Rainforest Study*. (Australian Government Publishing Service: Canberra).

Ødegaard, F. & Diserud, O.H. 2011. Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park (Queensland, Australia). *Memoirs of the Queensland Museum-Nature* 55(2): 359-374.

Olson, D.M. 1994. The distribution of leaf-litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology* **10**: 129-150.

Pyrcz, T.W. & Wojtusiak, J. 2002. The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Merida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography* **11**: 211-221.

Robertson, H.G. 2002. Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodiversity and Conservation* **11**: 1637-1652.

Samson, D.A., Rickart, E.A. & Gonzales, P.C. 1997. Ant diversity and abundance along an elevational gradient in the Philippines. *Biotropica* **29**: 349-363.

Sanders, N.J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography* **25**: 25-32.

Sanders, N.J., Lessard, J.-P., Fitzpatrick, M.C. & Dunn, R.R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* **16**: 640-649.

Sanders, N.J., Moss, J. & Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography* **12**: 93-102.

Shattuck, S. & Barnett, N. 2001. Australian Ants Online: The Guide to Australian Ant Fauna. Published at http://www.ento.csiro.au/science/ants/.

SPSS Inc. 2004. SPSS for Windows Rel. 13.0. Chicago.

Williams, G. 2002. A taxonomic and biogeographic review of the invertebrates of the Central Eastern Rainforest Reserves of Australia (CERRA) World Heritage Area, and adjacent regions. Technical Reports of the Australian Museum **16**: 1-2008.

Wilson, R., Trueman, J., Williams, S. & Yeates, D. 2007a. Altitudinally restricted communities of Schizophoran flies in Queensland's Wet Tropics: vulnerability to climate change. *Biodiversity and Conservation* **16**: 3163-3177.

Wilson, R.J., Gutierrez, D., Gutierrez, J. & Monserrat, V.J. 2007b. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**: 1873-1887.

APPENDIX 1. The distribution of ant species across the five altitudinal zones sampled during the IBISCA project, based upon all sampling methods and seasons. Letters indicate the replicate plots from which the species were recorded within altitudinal zone. Distributions based on the occurrence of wingless workers and ergatoid queens, except for the last six species which were represented only by alate or dealate queens.

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Amblyopone australis	B D	A B C D	A B C D	A B C D	A B C D
Anonychomyrma QM3	A B C D	A B C D	A B C D	A B C D	B D
Hypoponera IBISCA1	A B	A B C D	B D	A B C D	C
Monomorium IBISCA4	A B C	A B C D	A B C D	A B C D	A B C D
Myrmecina QM1	B	A C	A B C D	A B C D	A B C D
Pheidole IBISCA2	A B C D	A B C D	A B C D	A B C D	C
Sphinctomyrmex IBISCA1	A B	C	C	D	C
Tapinoma IBISCA4	A B	A C	C	B	B
Pheidole IBISCA8	D		C	B	C D
Amblyopone IBISCA1	D			B	A
Tapinoma IBISCA3	A C				C
Anonychomyrma IBISCA1	A B C D	A B C D	A B C D	A C D	
Camponotus IBISCA3	C	B D	A B C	A C D	
Carebara IBISCA1	A B C D	A B C D	A B C D	A D	
Crematogaster IBISCA1	A B C D	A B C D	A B C D	A B C D	
Discothyrea IBISCA3	A B C D	A B C D	A B C	A	
Hypoponera IBISCA2	A B C D	A B C D	A B C D	B C D	
Hypoponera IBISCA3	B	A B	B C	A B	
Hypoponera IBISCA4	A B	A B	A B C	A B D	
Leptogenys hackeri	A B C	A	A B C D	A D	
Leptomyrmex cnemidatus	A B C D	A B C D	A B C D	A B C D	
Leptomyrmex nigriventris	A B C D	C D	A B C D	A B D	
Mayriella abstinens	A B C D	A B C D	A B C D	D	
Mayriella overbecki	A B D	A B C D	A B C D	A D	
Monomorium tambourinense	A B C D	A B C D	A B C D	A B C D	
Notostigma foreli	A B C D	C D	A B C	A	
Orectognathus versicolor	A B C D	A B C D	A B C D	A D	
Pheidole IBISCA1	A B C D	A B C D	A B C D	A B C D	
Pheidole IBISCA3	B D	A B C D	A B C D	A B D	
Polyrhachis IBISCA1	A B C D	A B C D	A B C D	A D	
Polyrhachis IBISCA3	A B C D*	B C D	C	A B	
Ponera leae	A B C	B C D	A B C D	A B C D	

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Prionopelta robynmae	A B C D	A B C D	A B C D	A D	
Pristomyrmex quadridentatus	A B	A B C	A B C D	A C D	
Pristomyrmex wheeleri	B C	A	B	A D	
Rhytidoponera croesus	A B	A B C D	A B C D	A B C D	
Solenopsis IBISCA1	A B C D		A D	A B C D	
Hypoponera IBISCA6	A B	B		C D	
Pheidole megacephala	A C D	A B		B	
Anillomyrma IBISCA1	A B C D	A B C D	A B C D		
Cerapachys IBISCA2	A B	A C D	C		
Heteroponera IBISCA2	A B C	A C D	B C		
Iridomyrmex IBISCA2	B	A	D		
Leptogenys anitae	A B C D	A B C D	A B C D		
Notoncus capitatus	A B C D	A B C D	A D		
Orectognathus rostratus	B C D	A C D	A		
Paraparatrechina IBISCA2	A B C D	A B C	A		
Pheidole IBISCA4	A B C D	A B C D	A		
Pheidole IBISCA6	A B C D	A B C D	D		
Podomyrma IBISCA2	A B C D	A B D	A B		
Podomyrma IBISCA8	A B C	B	A		
Polyrhachis IBISCA4	A D	A	A B C D		
Prolasius IBISCA3	A B C D	A B C D	A B		
Rhytidoponera chalybaea	A B C D	A B C D	A B C D		
Rhytidoponera victoriae	A B C D	A B C D	A B C D		
Stigmacros major	A C D	A C	B C		
Strumigenys denteras	B C	A B D	A		
Technomyrmex IBISCA1	A B C	A C D	A B C D		
Orectognathus phyllobates	C D		A B		
Podomyrma IBISCA5	A		A C D		
Camponotus mackayensis	A B C D	A B C D			
Carebara IBISCA2	A B C D	B C D			
Colobostruma biconvexa	A C D	C			
Leptogenys mjobergi	A B C	A B C D			
Leptomyrmex burwelli	A B C D	A B C D			
Lordomyrma IBISCA1	A B	C D			
Monomorium IBISCA5	A B C D	D			

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Monomorium IBISCA6	B	D			
Pachycondyla porcata	A B C D	C D			
Nylanderia IBISCA1	A B C D	A B C D			
Pheidole IBISCA7	A B C D	D			
Platythyrea parallela	A C D	C			
Podomyrma IBISCA3	A D	A B D			
Prolasius IBISCA5	A B C D	D			
Prolasius IBISCA7	A B	B D			
Rhopalomastix IBISCA1	A C	B			
Rhopalothrix orbis	A C D	B			
Stigmacros barretti	C	B C D			
Tapinoma IBISCA1	B C D	A B C D			
Acropyga pallida	A B C				
Anisopheidole IBISCA1	A C D				
Camponotus IBISCA1	B C D				
Camponotus IBISCA2	A D				
Camponotus IBISCA4	A C				
Cerapachys IBISCA1	A				
Cerapachys IBISCA4	A D				
Cerapachys IBISCA5	C				
Cerapachys IBISCA6	B				
Colobostruma sisypha	B C				
Crematogaster IBISCA2	A B D				
Crematogaster IBISCA3	A B C D				
Crematogaster IBISCA4	A				
Eurhopalothrix australis	A				
Iridomyrmex IBISCA1	B D				
Iridomyrmex IBISCA3	A				
Leptogenys sjostedti	A B C D				
Leptomyrmex rufipes	D				
Lordomyrma IBISCA2	A				
Mayriella spinosior	A B C D				
Myrmecia nigrocincta	A B C				
Ochetellus IBISCA1	D				
Ochetellus IBISCA3	C				

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Orectognathus mjobergi	A				
Orectognathus robustus	B				
Pachycondyla australis	A C D				
Paraparatrechina IBISCA3	A D				
Paratrechina longicornis	D				
Pheidole IBISCA10	A B C D				
Pheidole IBISCA9	B				
Plagiolepis IBISCA2	D				
Podomyrma IBISCA6	B				
Podomyrma IBISCA7	D				
Polyrhachis IBISCA5	C D				
Polyrhachis IBISCA6	C				
Polyrhachis clio	C D				
Polyrhachis ornata	B				
Polyrhachis pilosa	A C D				
Probolomyrmex greavesi	C				
Stigmacros IBISCA2	A				
Stigmacros IBISCA4	C				
Cryptopone IBISCA1		A B	A B C D	A B C D	A B C D
Prolasius IBISCA1		A B C D	A B C D	A B C D	A B C D
Strumigenys perplexa		B C D	A B C D	A B C D	A B C D
Cryptopone IBISCA2		C	B		C
Discothyrea IBISCA1		A B C D	B C D		C
Heteroponera IBISCA1		C D	B C		A B D
Monomorium IBISCA1		A B D	D		A C D
Prolasius IBISCA6		D		A B C	A B C D
Monomorium nigriceps		A	B	A D	
Myrmecorhynchus IBISCA1		A B C D	A B C D	A B C D	
Paraparatrechina IBISCA4		A B C D	B C D	B D	
Prolasius convexa		A B C D	A B C D	A B C D	
Onychomyrmex IBISCA1		D		D	
Cerapachys IBISCA3		C D	D		
Hypoponera IBISCA5		A C D	D		
Hypoponera IBISCA7		A B	D		
Ochetellus IBISCA2		A	B		

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Pheidole IBISCA5		A B C	A B C D		
Prolasius IBISCA2		A C D	A B C D		
Strumigenys harpyia		A B C D	A B C D		
Tapinoma IBISCA2		A B	A B		
Teratomyrmex greavesi		A C	A		
Bothriomyrmex IBISCA1		A			
Camponotus IBISCA5		C			
Colobostruma froggatti		C			
Discothyrea IBISCA4		C D			
Machomyrma IBISCA1		D			
Plagiolepis IBISCA1		C D			
Podomyrma IBISCA4		A C			
Colobostruma australis			C	C D	
Orectognathus antennatus			A B C D	A B C D	
Podomyrma IBISCA1			A B C	B C D	
Sphinctomyrmex IBISCA2			D	B	
Monomorium IBISCA3			A B C D		
Myopias chapmani			D		
Podomyrma IBISCA9			D		
Strumigenys belua			A		
Strumigenys tisisyx			D		
Tetramorium simillimum			D		
Discothyrea IBISCA2				A C D	A B C D
Monomorium IBISCA2				B	A B C D
Myrmecorhynchus IBISCA2				A B C	A B D
Notoncus spinisquamis				A B	B C D
Technomyrmex IBISCA2				A D	A B
Leptogenys excisa				C	
Myrmecia brevinoda				A	
Orectognathus elegantulus				A B D	
Pachycondyla pachynoda				A B C	
Pheidole IBISCA12				C	
Pachycondyla IBISCA3					D

APPENDIX 1. continued ...

Ant Species	Elevational zone				
	300 m	500 m	700 m	900 m	1100 m
Queens only					
Amplyopone IBISCA2 *	B				
Amplyopone IBISCA3*		B			
Cardiocondyla IBISCA1*		A		A B	
Metapone IBISCA1*	B C D			D	
Metapone IBISCA2*		D			
*Myopias tasmaniensis**		C			

Australian goblin spiders of the genus *Opopaea* Simon, part 1. The species of the IBISCA-Queensland Project at Lamington National Park (Araneae: Oonopidae)

Barbara C. BAEHR

Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia. Email: barbara.baehr@qm.qld.gov.au

CSER, School of Environmental and Life Sciences, University of Newcastle, Callaghan, NSW 2308, Australia.

Citation: Baehr, B.C. 2011 12 20. Australian Goblin Spiders of the genus *Opopaea* Simon, part 1. The species of the IBISCA-Queensland Project at Lamington National Park (Araneae: Oonopidae). *Memoirs of the Queensland Museum – Nature* 55(2): 413-437. Brisbane. ISSN 0079-8835.

ABSTRACT

The IBISCA-Queensland Project, an intensive survey of invertebrates along an altitudinal gradient within subtropical rainforest at Lamington NP in Queensland, Australia, revealed eight new species of the goblin spider genus *Opopaea* Simon, 1891 including: *O. antoniae* sp. nov., *O. jonesae* sp. nov., *O. leica* sp. nov., *O. olivernashi* sp. nov., *O. rogerkitchingi* sp. nov., *O. sown* sp. nov., *O. speighti* sp. nov. and *O. yukii* sp. nov., each described from both sexes. A key is provided for these Australian *Opopaea* species and their altitudinal distributions are discussed. ❐ *Opopaea, Lamington National Park, Goblin Spiders, IBISCA*

The IBISCA-Queensland Project, led by Prof. Roger Kitching, was an international collaborative project that aimed to determine groups of organisms that can serve as indicators of climate change at different altitudinal zones in the rainforest of Lamington National Park. During the fieldwork of the IBISCA-Queensland Project, conducted between 2006 and 2008, eight new species of goblin spiders of the genus *Opopaea* Simon were found. *Opopaea* belongs to the *Oonopidae*, a megadiverse spider family currently with 755 described species in 83 genera and approximately 2500 expected species worldwide (Platnick 2009). These small goblin spiders (0.5–4.0 mm in body length) are regularly found in most terrestrial habitats, particularly in litter, under bark and even in the forest canopy. Goblin spiders occur throughout mainland Australia as well as Tasmania.

Until relatively recently only 13 indigenous Australian species have been described in the genera *Camptoscaphiella* Caporiacco, *Gamasomorpha* Karsch, *Grymens* Harvey, *Oonops* Templeton, *Opopaea* and *Orchestina* Simon (Harvey 1987; Harvey & Edward 2007; Hickman 1932, 1950; Koch 1873; Rainbow 1920; Simon 1908). In addition, the introduced species *Oonops pulcher* Templeton, 1835 has been recorded from Tasmania (Hickman 1979). Recent publications have revealed another 21 Australian goblin spiders species of the genera *Cavisternum* Baehr, Harvey & Smith, *Pelicinus* Simon and *Xestaspis* Simon (Baehr, Harvey & Smith 2010; Ott & Harvey 2008a, b) as part of a world-wide revision of the family Oonopidae conducted by the "Goblin Spider PBI" project (see http://research.amnh.org/oonopidae/). Australian museum collections contain at least another 500 new goblin spider species. However, the discovery of numerous new spider taxa from Australia is not astonishing, as revisions of ground-dwelling spiders over

recent years have discovered a huge number of new taxa across a wide variety of spider families (e.g. Zodariidae: Baehr 2008; Prodidomidae: Platnick & Baehr 2006; Zoropsidae: Raven & Stumkat 2005; Pararchaeidae: Rix 2006).

Species of *Opopaea* are united by their orange-brown colouration, lentil-like abdominal scutae and huge, club-shaped palpal patellae. *Opopaea* is one of the most diverse Australian goblin spider genera but only three species have been described to date; one species from South Australia (Hickman 1950) and two blind, troglobitic species from Western Australia (Harvey & Edward 2007). The description of eight new *Opopaea* species collected during the IBISCA project is the first revisionary paper on the Australian goblin spiders of the genus *Opopaea* as part of the 'Goblin Spider PBI' project. It is likely that the rainforest *Opopaea* species described here are short-range endemics with very small distributions (Harvey 2002) and may prove to be important taxa for monitoring the effects of climate change.

MATERIAL AND METHODS

Large areas of Lamington National Park, situated in south-eastern Queensland (Fig. 63), are covered with subtropical rainforest, ranging from lowland rainforest at around 300 metres above sea level (m a.s.l.) to cool, misty, *Nothofagus* dominated rainforest at 1100 m a.s.l. During the IBISCA-Queensland Project (Kitching *et al.* 2011), intensive surveys were undertaken at four plots (A, B, C and D) within each of five altitudinal zones at approximately 300, 500, 700, 900 and 1100 m a.s.l. from 2006 to 2008. Precise location details and elevations of the main IBISCA plots, as well as those of a number of supplementary plots where additional collections of *Opopaea* specimens are presented in Table 1 (see also Kitching *et al.* 2011).

Specimens of *Opopaea* were collected using a range of methods including pitfall traps, litter extractions and bark spraying. The latter technique involved thoroughly spraying the trunks of large trees using hand-held cans of Mortein Fast Knockdown® insecticide, directing the jet of spray from the base to as far as possible up the trunk. Falling insects were collected on a rectangular sheet of rip-stop nylon (160 x 105 cm) placed at the base of each tree (see Burwell & Nakamura 2011 for more details).

Specimens were examined using a LEICA MZ16A microscope. Photomicrographic images were produced using a Leica DFC 500 and the software program AutoMontage Pro Version 5.02 (p). SEM's were taken with a Hitachi S530. Descriptions were generated with the aid of the PBI descriptive goblin spider database and shortened where possible. The map was created with the simpler mapper of the PBI Goblin Spider Project; http://research.amnh.org/pbi/maps/. All measurements are in millimetres. All specimens are deposited in the Queensland Museum. Morphological terminology for the female genitalia follows Burger (2010). Abbreviations used in the text and figures are: ALE, anterior lateral eye(s); C/L, connection of femur/patella; Ch, broad triangular chitinised area of female genitalia; GAp, globular appendix of female genitalia; L, length of male patella; Na, nail-like process of female genitalia; PLE, posterior lateral eye(s); PME, posterior median eye(s); PSc, paddle-like sclerite of female genitalia; W, width of male patella; W/L, male patella width/length. Abbreviations for collectors used in the material examined are: AM, A. Marcora; AN, A. Nakamura; CB, C. Burwell; DP, D. Putland; FT, F. Turco; GM, G. Monteith; GT, G. Thompson; KS, K. Staunton; SW, S. Wright. Specimens in the material examined section are grouped according to the IBISCA-Queensland study plots, with increasing altitude and plot number, followed by additional material collected from outside

TABLE 1. Latitude and longitude (in decimal degrees), and precise elevation (metres above sea level) of the main IBISCA-Queensland survey plots and supplementray IBISCA-Queensland plots from which *Opopaea* specimens examined in this study were collected.

IBISCA-Qld plot name	Latitude (°S)	Longitude (°E)	Elevation (m a.s.l.)
Main plots			
300A	28.148	153.137	267
300B	28.155	153.139	282
300C	28.151	153.138	260
300D	28.142	153.133	248
500A	28.216	153.142	560
500B	28.212	153.141	514
500C	28.210	153.139	474
500D	28.207	153.137	471
700A	28.188	153.121	746
700B	28.192	153.124	775
700C	28.193	153.128	748
700D	28.204	153.129	748
900A	28.234	153.141	904
900B	28.238	153.145	950
900C	28.240	153.149	944
900D	28.227	153.131	920
1100A	28.258	153.159	1141
1100B	28.259	153.162	1142
1100C	28.260	153.167	1106
1100D	28.262	153.170	1140
Supplementary			
700CKA	28.237	153.152	720
850	28.215	153.126	841
1000	28.247	153.149	995

the IBISCA transect (for precise locality and altitude information for the IBISCA plots refer to Table 1).

OPOPAEA SPECIES OF LAMINGTON NATIONAL PARK AND THEIR ALTITUDINAL PREFERENCES

In total 255 specimens of *Opopaea* were collected during the IBISCA-Queensland project. Specimens of *Opopaea* were collected from all five altitudinal zones (300 m a.s.l.: 83 specimens, 500 m: 59, 700 m: 71, 900 m: 21, 1100 m: 21). The *Opopaea* species from the rainforest of Lamington NP are all extremely similar in their body shape (Figs 1–10). They differ only in their eye size, the arrangement of sternal setae between coxa IV (Fig. 60 arrow) and their genitalia. Although the genus *Opopaea* is found throughout the range of altitudes surveyed during the IBISCA-Queensland project, individual *Opopaea* species appear to have restricted altitudinal distributions (Fig. 64, Table 2), although there is insufficient data to enable statistical analysis of the species' altitudinal preferences.

The *Opopaea* species treated here can be divided in 2 groups according to their eye size (Table 2):

Species with small (diameter of ALE less than 0.045 mm), subequal eyes (*O. sown* sp. nov., *O. jonesae* sp. nov., *O. rogerkitchingi* sp. nov.). These are evidently litter-inhabiting species that were collected only by pitfall traps or litter extraction. This group of species showed distinct altitudinal zonation with *O. sown* collected only from the lowest elevations (300 m a.s.l.), *O. jonesae* found at mid-elevations (500-900 m a.s.l.), most commonly between 500 and 700 m a.s.l, and *O. rogerkitchingi* found at mid to high elevations (700–1100 m a.s.l.), most commonly at the highest elevation of 1100 m a.s.l. (Fig. 64, oval circles).

Species with large eyes, nearly twice as large as those of the former group (*O. antoniae* sp. nov., *O. leica* sp. nov., *O. olivernashi* sp. nov., *O. speighti* sp. nov., *O. yukii* sp. nov.). Whereas *O. yukii* and *O. antoniae* were collected only on tree trunks by bark spraying, *O. olivernashi*, *O. leica* and *O. speighti* are apparently litter-inhabiting species (collected by pitfall traps or litter extraction). *Opopaea yukii*, the only dorso-ventrally flattened, large-eyed species, appeared in high numbers at all altitudes, except at 1100 m where it was replaced by *O. antoniae* (which occurs from 700–1100 m

TABLE. 2 *Opopaea* species from Lamington National Park characterised by: lateral habitus, eye size, including the diameter of the anterior lateral eyes (ALE), microhabitat, IBISCA-Queensland elevational zones from which they were collected and the total number of specimens examined.

Species	Lateral habitus	Eye size	ALE diameter (mm)	Main habitat	Elevational range (m a.s.l)	Number of specimens
O. rogerkitchingi	flattened	small	0.034	litter	700-1100	22
O. jonesae	normal	small	0.040	litter	500-900	46
O. sown	flattened	small	0.041	litter	300	9
O. speighti	normal	large	0.048	litter	900-1000	5
O. olivernashi	normal	large	0.077	litter	500-700	15
O. leica	normal	large	0.069	litter	300-700	11
O. antoniae	normal	large	0.077	bark	700-1100	11
O. yukii	flattened	large	0.076	bark	300-900	136

a.s.l.) presumably because of the very mossy bark of trees at 1100 m. The large-eyed litter species *O. olivernashi* (500–700 m a.s.l.), *O. leica* (300-700 m a.s.l.) and *O. speighti* (900-1000 m a.s.l.) apppeared to show distinct altitudinal preferences though only relatively few specimens of each species were collected.

This study demonstrates that particular *Opopaea* species have specific habitat preferences along the IBISCA altitudinal gradient, especially *O. antoniae*, *O. rogerkitchingi* and *O. speighti* which are largely restricted to high elevations like a number of orsolobid spider species (Baehr *et al.* 2011) and hence are a good potential target group for monitoring the effects of future climate change.

SYSTEMATICS

Family Oonopidae Simon, 1890

Opopaea, Simon 1891

Opopaea Simon, 1891:560 (type species by monotypy *Opopaea deserticola* Simon)

Diagnosis and description see Platnick & Dupérré (2009).

Diagnosis. Males of *Opopaea* can be easily recognised by their big, club-shaped palpal patella which originates sub-basally or medially from the palpal femur (Figs 20–43) and the strong, tooth-like projection at the anteromedian tip of the endites (Fig. 60 white arrow). Females are more difficult to characterise but can be distinguished by the wide triangular chitinised area near the genital opening (Fig. 44) and the internal t-shaped or paddle-like sclerite situated near the genital opening (Fig. 51). All *Opopaea* species from Lamington NP differ from *Opopaea deserticola* Simon in having a high rebordered clypeus and the ALE separated from the edge of the carapace by their radius or more.

Description. *Opopaea* species collected from Lamington National Park including *O. antoniae* sp. nov., *O. jonesae* sp. nov., *O. leica* sp. nov., *O. olivernashi* sp. nov., *O. rogerkitchingi* sp. nov., *O. sown* sp. nov., *O. speighti* sp. nov., *O. yukii* sp. nov. share the following characters: *Male*: *Carapace* ovoid in dorsal view without any pattern (Figs 1–8), anteriorly narrowed to 0.49 times its maximum width or less, surface of elevated portion of pars cephalica smooth, sides striated, thorax without depressions, fovea absent, without radiating rows of pits; lateral

margin straight, rebordered, without denticles; non-marginal pars cephalica setae needle-like, present in u-shaped row; non-marginal pars thoracica setae absent; marginal setae absent. *Clypeus* rebordered, curved downwards in front view, vertical in lateral view, high, ALE separated from edge of carapace by their radius or more. *Chilum* absent. *Eyes* six, well-developed, posterior eye row straight from above, procurved from front. *Sternum* longer than wide, uniform, fused to carapace, with radial furrows between coxae I-II, II-III, III-IV, furrow with rows of small pits, microsculpture only in furrows, rest of surface smooth, anterior margin unmodified, posterior margin not extending posteriad of coxae IV, distance between coxae approximately equal, lateral margin with infra-coxal grooves and anterior and posterior openings; setae needle-like, originating from small pits. *Mouthparts* Chelicerae straight, directed medially, anterior face unmodified; without teeth on both promargin and retromargin; without tooth-like projections; paturon inner margin with pairs of enlarged setae, distal region unmodified. Labium triangular, fused to sternum, anterior margin indented at middle. Endites, serrula in single row, anteromedian tip with one strong, tooth-like projection. *Abdomen* ovoid, rounded posteriorly, soft portions white; book lung covers without setae, anterolateral edge unmodified. Posterior spiracles connected by groove. Pedicel tube short, ribbed, with small, dorsolateral, triangular extensions; scuto-pedicel region with paired curved scutal ridges, scutum not extending far dorsad of pedicel. Dorsal scutum strongly sclerotised, without colour pattern, covering full length of abdomen, no soft tissue visible from above, not fused to epigastric scutum, surface punctate, anterior half without projecting denticles. Epigastric scutum strongly sclerotised, surrounding pedicel, not protruding, small lateral sclerites absent. Postepigastric scutum strongly sclerotised, long, semicircular, covering nearly full length of abdomen, fused to epigastric scutum, anterior margin unmodified, with long posteriorly directed lateral apodemes. Spinneret scutum present as incomplete ring with fringe of short setae. Supra-anal scutum absent. Dorsum of epigastric and postepigastric areas with uniform setae. Interscutal membrane with setae. Colulus represented only by 2 setae. *Legs* without colour pattern; patella plus tibia I shorter than carapace, no scopula. Leg spines absent. Tarsi I to IV without inferior claw. *Genitalia* Epigastric region with sperm pore small, oval, situated at level of anterior spiracles. *Palp* trochanter minute, with ventral projection; femur triangular with wide basis, attaching to patella sub-basally to medially; patella much larger than femur, club-shaped; tibia small; cymbium and bulb at least partly fused, bulb 1 to 1.5 times as long as cymbium, slender, distal part with dorsal fenestra.

Female: As in male except as noted. Endites without anteromedian tooth-like projection. Epigastric and postepigastric scutum not fused. Genitalia in ventral view: Between genital opening and grove, connecting posterior spiracles, is a wide triangular chitinised area, situated close to genital opening (Figs 44, 46, 48, 50, 52, 54, 56, 58). Genitalia in dorsal view: t-shaped or paddle like sclerite situated near genital opening (Figs 45, 47, 49, 51, 53, 55, 57, 59) with nail-like process (Na) fitting into posterior situated globular appendix (GAp).

KEY TO SPECIES OF *OPOPAEA* OF LAMINGTON NP

1. Males 2
— Females 9
2. Eyes small, subequal, PME diameter less than 0.04 mm (Figs 2, 5, 6) 3
— Eyes large, ALE or PME largest, PME at least 0.05 mm (Figs 1, 3, 4, 7, 8) 5
3. Sternum swollen between coxae IV 4
— Sternum not swollen between coxae IV . . . . . *O. sown* sp. nov.

4. Setae between coxae IV arranged in a circle and directed centrally ..... *O. rogerkitchingi* sp. nov.
– Setae between coxae IV arranged in a longitudinal band ..... *O. jonesae* sp. nov.
5. Carapace and abdomen flat in lateral view (Fig. 9) ..... *O. yukii* sp. nov.
– Carapace and abdomen slightly elevated in lateral view (Fig. 10) 6
6. Sternum between coxae IV with posterior swelling and hair tuft (Fig. 60)..... O. leica sp. nov.
– Sternum between coxae IV without posterior swelling and hair tuft (Fig. 11) 7
7. Palpal bulb and cymbium without retrolateral seam (Figs 43)..... *O. speighti* sp. nov.
– Palpal bulb and cymbium with retrolateral seam (Figs 22, 25)..... 8
8. Palpal femur connected to patella sub-basally, C/L 0.37 (Figs 20–22) . . *O. olivernashi* sp. nov.
– Palpal femur connected to patella medially, C/L 0.48 (Figs 23–25) . . . *O. antoniae* sp. nov.
9. Eyes small, subequal, PME diameter less than 0.04 mm (Figs 2, 5, 6) 10
– Eyes large, ALE or PME largest, PME at least 0.05 mm (Figs 1, 3, 4, 7, 8) 12
10. Chitinised area of female genitalia in ventral view a broad band, posterior knob-like extension square (Fig. 54) . *O. rogerkitchingi* sp. nov.
– Chitinised area of female genitalia in ventral view a narrow band, posterior knob-like extension triangular (Figs 50, 52)..... 11
11. Globular appendix (see Fig. 47, GAp) without hood but with keel-like extension (Fig. 51) ..... *O. sowu* sp. nov.
– Globular appendix with hood and triangular posterior extension (Fig. 53) ..... *O. jonesae* sp. nov.
12. Carapace and abdomen flat in lateral view (Fig. 9); chitinised area of female genitalia a narrow band with small sinuous posterior extension (Fig. 56) ..... *O. yukii* sp. nov.
– Carapace and abdomen slightly elevated in lateral view (Fig. 10); chitinised area of female genitalia broadly triangular (Figs 44, 46, 48, 58) 13
13. Globular appendix embedded in chitinised area which has a small dorsally bent median tip (Fig. 47) ..... *O. antoniae* sp. nov.
– Globular appendix not embedded in chitinised area (Figs. 45, 49, 59)..... 14
14. Globular appendix divided into hood and v-shaped extension (Fig. 45) ..... *O. olivernashi* sp. nov.
– Globular appendix divided into hood and small globular extension (Figs 49, 59) . . 15
15. Chitinised area of female genitalia with narrow triangular posteriorly directed extension (Fig. 58) ..... *O. speighti* sp. nov.
– Chitinised area of female genitalia with broad triangular posteriorly directed extension (Fig. 48) ..... *O. leica* sp. nov.

Opopaea antoniae sp. nov.
(Figs 1, 11–14, 16–19, 23–25, 46, 47, 63)

Etymology. Named for Antonia Burwell-Rodriguez, daughter of Chris Burwell, Senior Curator of Entomology at the Queensland Museum, in recognition of his contributions to ecology and taxonomy and to his daughter's love for little creatures.

Material. Holotype ♂, Queensland, Lamington NP, IBISCA 1100C, 28.206°S 153.167°E, 1106 m, 26 Oct 2006, CB, bark spray (PBI_OON 23239, QM S86315). **Other Material.** QUEENSLAND, IBISCA 700A: 1♀, 18 Jan 2008, AN, bark spray (PBI_OON 23353, QM S84085); 1♂, 1♀, 26 Sep 2008, GM, FT, bark spray (PBI_OON 23361, QM S86426). IBISCA 700C: 2♂, 2♀, 26 Sep 2008, GM, FT, bark spray (PBI_OON 23360, QM S86423). NEW SOUTH WALES, 1♀, 1♂ Wiangaree, Beach Picnic Area, 28.36666°S 153.1°E, 1050 m, 15 Dec 2008, GM, pyrethrum Nothofagus (PBI_OON 23341, QM S84083).

Diagnosis. *Opopaea antoniae* resembles *O. olivernashi* in colour and eye size. Females and males of *O. antoniae* can be separated from all other species of *Opopaea* known from Lamington NP by their small, round and darker brown book lung covers. Males of *O. antoniae* and *O. olivernashi* are the only Lamington species with a retrolateral seam between

the bulb and cymbium. Males of *O. antoniae* can be easily separated from *O. olivernashi* by their slimmer patella, the median connection to the femur (C/L= 0.48) and the slim bulb. Females of *O. antoniae* can be distinguished from all other *Opopaea* species by the broad triangular chitinised area (Ch) near the genital opening.

Description. *Male* (holotype, PBI_OON 23239). Total length 1.70. *Colour in alcohol*. Body yellow-brown, legs and palp pale orange, only patella reddish brown. *Carapace* pars cephalica slightly elevated in lateral view, with rounded posterolateral corners. *Clypeus* high, rebordered (Fig. 12) with four long setae in inverted v-shaped position. *Eyes* very large, ALE largest. ALE: 0.077; PME: 0.064; PLE: 0.055; Eye-group width: 0.226; PME oval, PLE circular; ALE separated by less than their radius, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME touching. *Abdomen* book lung covers small, round, darker brown than surrounding abdomen. *Legs* (trichobothria examined with SEM) tibiae I-IV with 3 dorsal trichobothria (Fig. 17), metatarsi I-IV with 1 dorso-distal trichobothrium (Fig. 16), base rounded, hood smooth. Tarsal claws I-IV striated with 5 strong ventral teeth (Figs 13-14). *Genitalia* (Figs 23-25): femur medially attached to patella (C/L= 0.48, Fig. 25); patella: W/L=0.58; L=0.280; W=0.162; C=0.134 (mm); cymbium ovoid in dorsal view, fused with bulb, but seam visible on retrolateral side, with distal patch of setae.

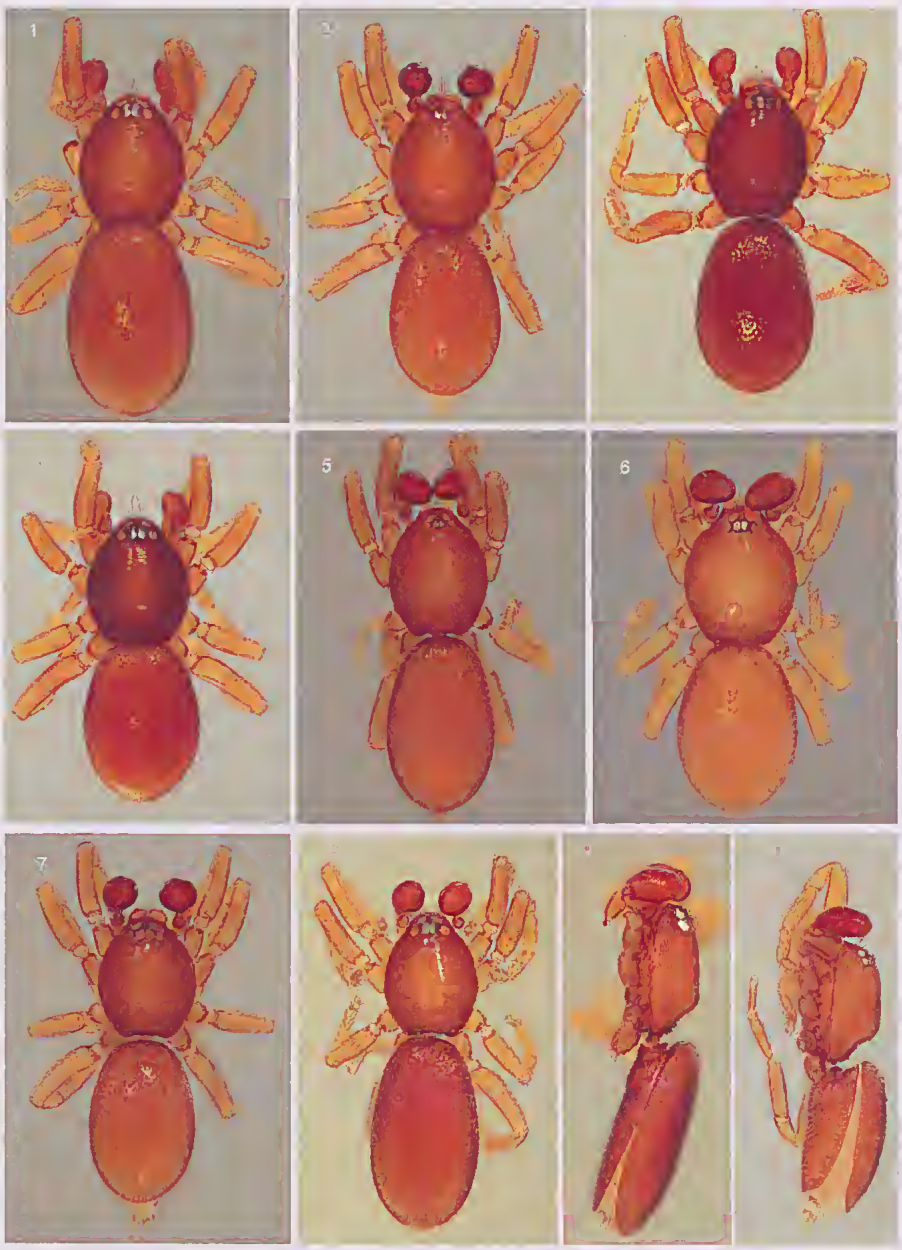
Female. (PBI_OON 23341) Total length 1.88. As in male except as noted. Eyes very large; ALE: 0.070; PME: 0.052; PLE: 0.045; Eye-group width: 0.207. *Genitalia* (Figs 46-47): Broad triangular chitinised area (Ch) in ventral view, with small dorsally bent median tip (arrow) in dorsal view; paddle-like sclerite (PSc) with thin straight arms bent at end; nail-like process (Na) large, well separated; globular appendix (GAp) globular embedded in chitinised area.

Distribution. This species is only known from the southeast corner of Queensland and north-eastern New South Wales (Fig. 63).

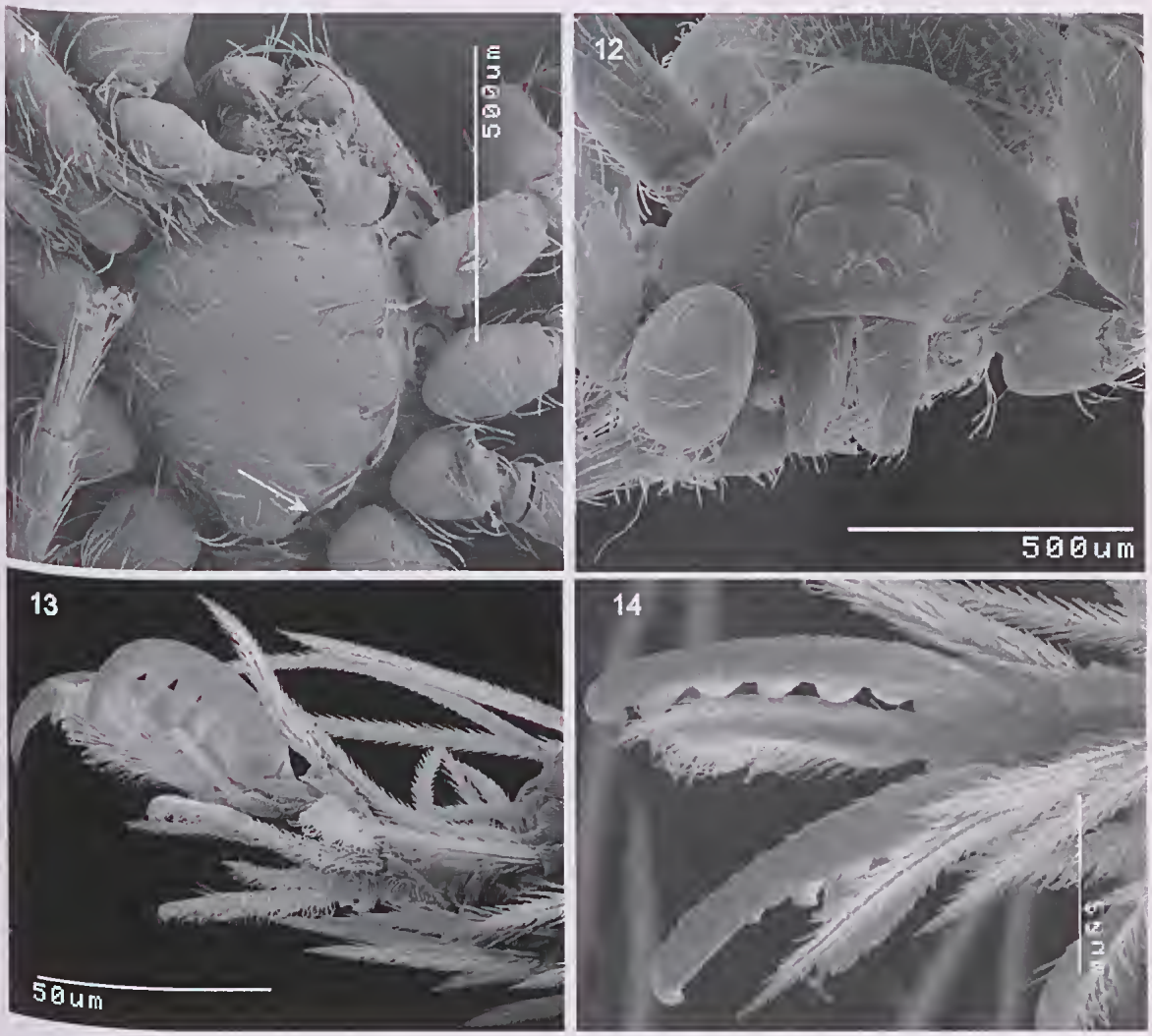
Opopaea jonesae sp. nov.
(Figs 2, 10, 29–31, 52, 53, 62, 63)

Etymology. A patronym in honour of Anne Jones, former Chair of the Queensland Museum Board, for her love of nature and her outstanding service and support of the Queensland Museum over many years.

Material. Holotype ♂, Queensland, Lamington NP, IBISCA, 700C, 28.193°S, 153.128°E, 748 m, 12–21 Feb 2007, KS, pitfall (PBI_OON 22751, QM S76160). PARATYPE, QUEENSLAND, 1♀, same data as holotype but (PBI_OON 23355, QM S87075). OTHER MATERIAL, QUEENSLAND, 1♂, Lamington NP, 0.6 km N of Ballanjui Falls, 28.207°S, 153.203°E, 460 m, 19 Mar 2008, SW, AN, berlesate sifted litter (PBI_OON 23245, QM S86327). IBISCA 500A: 3♂, 12–21 Feb 2007, KS, pitfall (PBI_OON 22709, QM S76055); 1♂, 12–21 Mar 2007, DP, KS, pitfall (PBI_OON 23322, QM S86401); 2♂, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23268, QM S86387), 1♂, same data (PBI_OON 23274, QM S86390). IBISCA 500B: 1♀, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23273, QM S86385). IBISCA 500C: 1♂, KS, pitfall (PBI_OON 22749, QM S76054); 1♂, 8 Oct 2006, BB (PBI_OON 22736, QM S75880); 1♂, 12–21 Mar 2008, DP, KS, pitfall (PBI_OON 23330, QM S866400); 2♂, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23265, QM S86381, PBI_OON 23276, QM S86386), 1♀, (PBI_OON 23265, QM S86381). IBISCA 500D: 1♂, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23264, QM S86382); 1♀, 1♂ same data (PBI_OON 23272, QM S86393). IBISCA 700B: 1♀, AN, leaf litter extract (PBI_OON 23263, QM S86339); 1♀, 1♂, 14–23 Jan 2007, KS, pitfall (PBI_OON 23240, QM S86311); 1♂, 12–21 Feb 2007, KS, pitfall (PBI_OON 22742, QM S76085); 1♀, 13–22 Mar 2007, DP, KS, pitfall (PBI_OON 23246, QM S86320); 1♀, 18 Jan 2008, SW, leaf litter extract (PBI_OON 23266, QM S86352); 2♀, 1♂, 26 Sep 2008, GM, FT, litter berlesate (PBI_OON 23358, QM S86429). IBISCA 700C: 1♀, 14–23 Jan 2007, KS, pitfall (PBI_OON 23241, QM S86309); 1♂, 12–21 Feb 2007, KS, pitfall (PBI_OON 23354, QM S87074); 2♀, 20 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23267, QM S86346, PBI_OON 23270, QM S86343). IBISCA 700CKD: 2♀, 22 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23253, QM S86318). IBISCA 700D: 1♂, 11–20 Oct 2006, KS, pitfall (PBI_OON 22715, QM S81116); 2♂, 13–22 Mar 2007, DP,



FIGS 1-10. *Opopaea* species of Lamington National Park. Male habitus, 1-8, dorsal; 9-10, lateral. 1, *O. antoniae* sp. nov. (PBI_23239); 2, *O. jonesae* sp. nov. (PBI_22751); 3, *O. leica* sp. nov. (PBI_23237); 4, *O. olivernashi* sp. nov. (PBI_23254); 5, *O. rogerkitchingi* sp. nov. (PBI_22772); 6, *O. sown* sp. nov. (PBI_22746); 7, *O. speighti* sp. nov. (PBI_23256); 8-9, *O. yukii* sp. nov. (PBI_06383); 10, *O. jonesae* sp. nov. (PBI_22751).



FIGS 11–14. *Opopaea antoniae* sp. nov. (PBI_OON 23360). 11, sternum ventral (arrow points to lateral margin with infra-coxal grooves and anterior and posterior openings); 12, carapace frontal; 13-14, tarsus IV, retrolateral (13) and dorsal (14) views.

KS, pitfall (PBI_OON 23248, QM S86319; PBI_OON 23249, QM S86322); 1♀, 2♂, 20 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23262, QM S86335). IBISCA 900D: 1♂, 12–21 Feb 2007, KS, pitfall (PBI_OON 22737, QM S76184); 1♂, 11–20 Mar 2007, DP, KS, pitfall (PBI_OON 23275, QM S86366). 2♀, 1♂, 0.5 km SSE Binna Burra Lodge, 28.198°S 153.190°E, 770 m, 18 Mar 2008, SW, AN, berlesate sifted litter (PBI_OON 23247, QM S86325).

Diagnosis. *Opopaea jonesae* resembles *O. rogerkitchingi* in colour and in having small eyes which are equal in size. Males of *O. jonesae* and *O. rogerkitchingi* have a slim bulb and a palpal patella with a median connection to the femur (C/L=0.51). Males of *O.*

jonesae can be easily separated by a longitudinal band of setae at the swollen posterior part of the sternum between coxae IV (Fig. 62) and the medially bent flagellate distal tip of the bulb. Females can be distinguished from those of *O. rogerkitchingi* by the narrow, widely triangular chitinised area near the genital opening.

Description. *Male* (holotype, PBI_OON 22751). Total length 1.41. *Colour in alcohol.* Body pale orange-brown, palpal patella reddish brown. *Carapace* pars cephalica slightly elevated in lateral view. *Clypeus* with few long setae in v-shaped position. *Eyes* small, subequal in size. ALE: 0.040; PME: 0.037; PLE: 0.034; eye quadrangle: 0.161, PME oval, PLE circular; ALE separated by their radius to diameter, ALE-PLE separated by less than ALE radius, PME touching for less than half their length, PLE-PME separated by less than PME radius. *Sternum* (Fig. 62) posterior part between coxae IV swollen, with longitudinal band of setae; other setae evenly scattered. *Abdomen.* Book lung covers large, ovoid. *Genitalia* (Fig. 29-31): patella big, club-shaped, W/L=0.54; connection to femur C/L= 0.51. L=0.305; W=0.166; C=0.155; cymbium completely fused with bulb, no seam visible, distal tip of bulb medially bent, flagellate.

Female. (paratype, PBI_OON 23355) Total length 1.60. As in male except as noted. *Eyes* ALE: 0.042; PME: 0.036; PLE: 0.033; eye quadrangle: 0.137. *Genitalia* (Figs 52, 53): Narrow chitinised area (Ch) with small posteriorly directed v-shaped extension in ventral view; dorsal view, paddle-like sclerite (PSc) with evenly bent arms; nail-like process (Na) not well separated; globular appendix (GAp) separated into two parts, anterior part small globular, posterior part with triangular tip, not embedded in chitinised area.

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

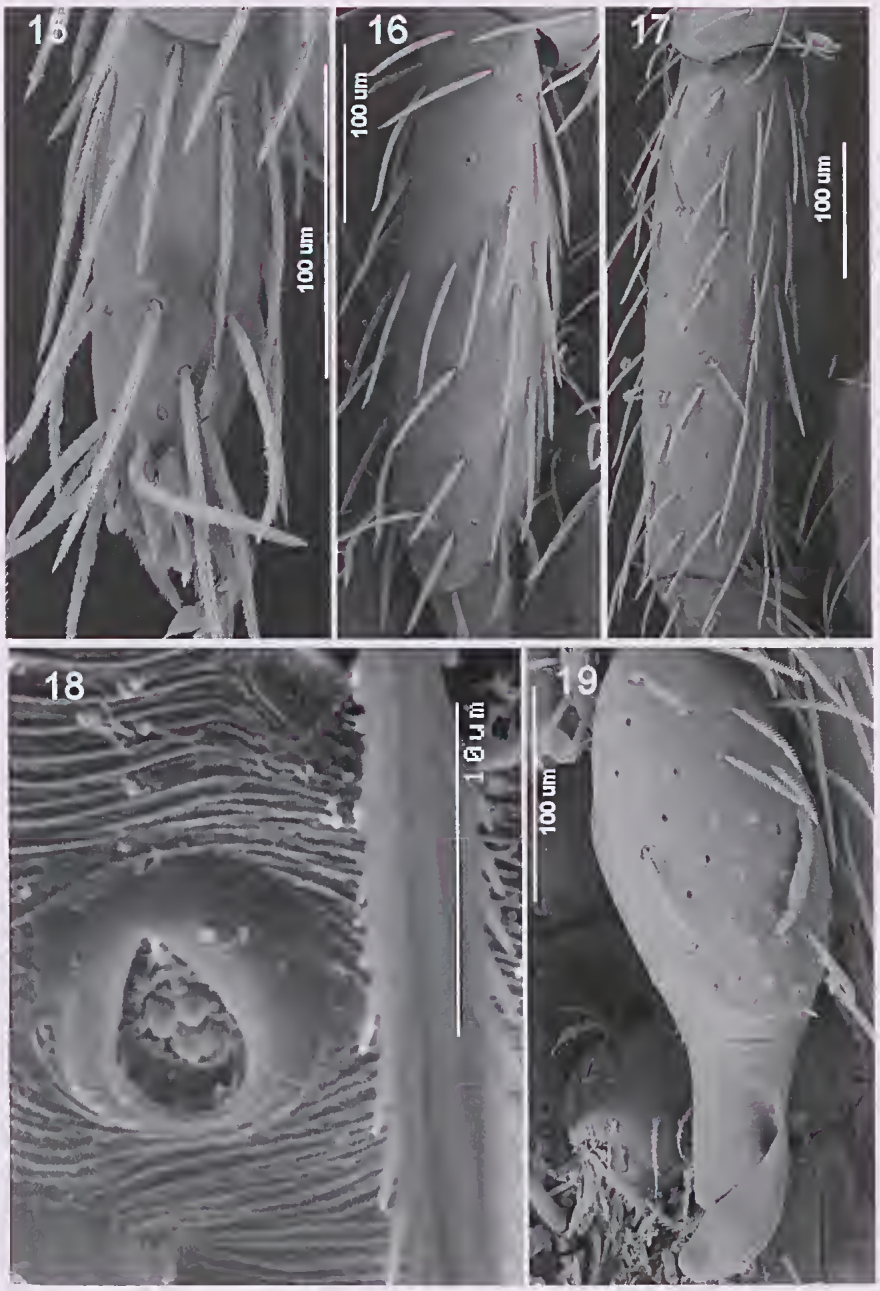
Opopaea leica sp. nov.
(Figs 3, 26–28, 48, 49, 60, 63)

Etymology. A patronym in honour of Leica Microsystems Pty Ltd, Australia and Dermot Allen the Product Manager-Division of Microscopy and Imaging, Sydney for their immense support in providing equipment for this taxonomic work.

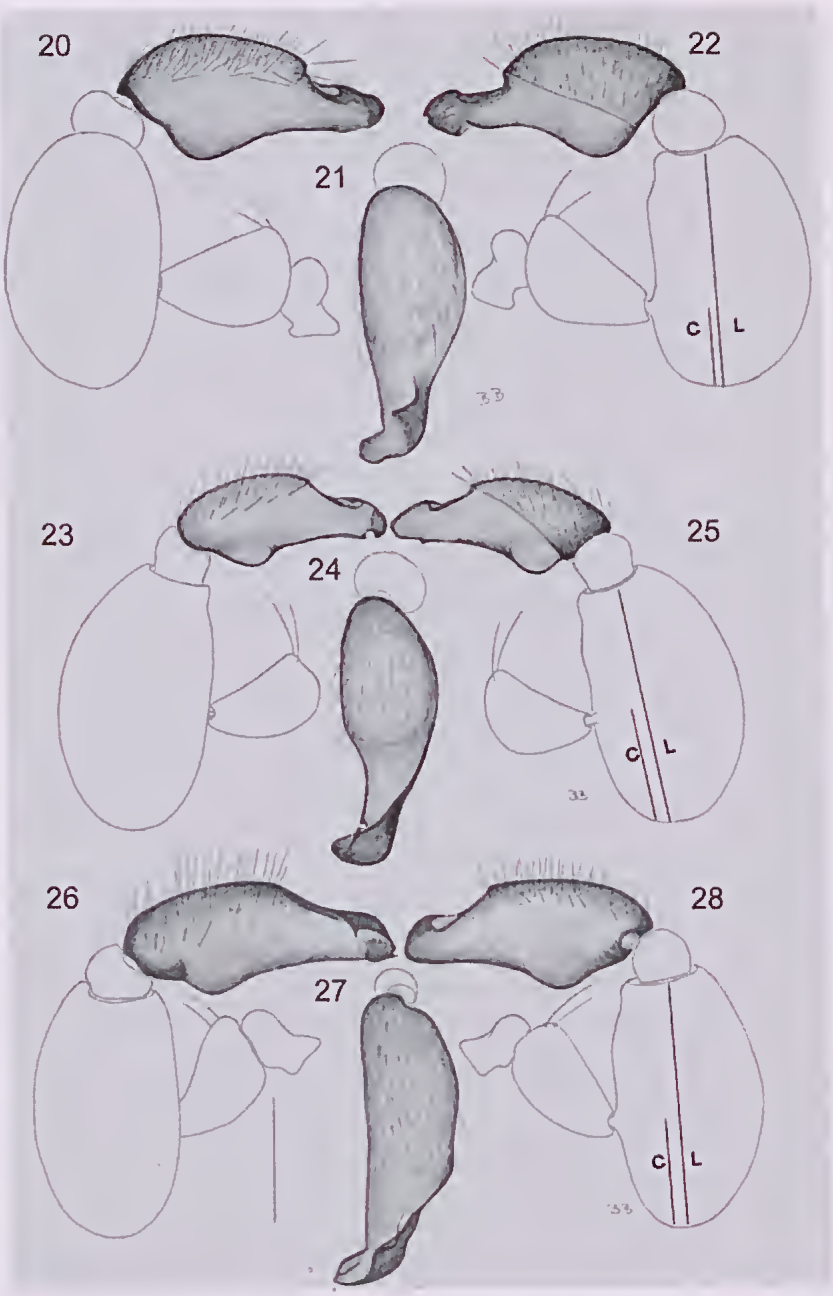
Material. Holotype ♂, Queensland, Lamington NP IBISCA, 700C, 28.193°S, 153.128°E, 748 m, 11–20 Oct 2006, KS, pitfall (PBI_OON 23237, QM S86307). PARATYPE, QUEENSLAND, 1♀, Lamington NP IBISCA, 700D, 28.204°S 153.129°E, 748 m, 20 Jan 2008, S. Wright, AN, leaf litter extract (PBI_OON 23282, QM S86336). OTHER MATERIAL, QUEENSLAND, IBISCA 300A: 2♂, 25 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23277, QM S86338). IBISCA 300C: 1 ♂, 18–23 Jan 2007, GM, fungus pitfall (PBI_OON 23243, QM S86310). IBISCA 700A: 1♀, 18 Jan 2008, AN, bark spray (PBI_OON 23293, QM S86391); 2♂, 13–22 Mar 2007, DP, KS, pitfall (PBI_OON 23251, QM S86317). IBISCA 700B: 1♂, 18 Jan 2008, AN, leaf litter extract (PBI_OON 23281, QM S86340); 1♂, (PBI_OON 23280, QM S86380). IBISCA 700D: 1♂, 20 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23356, QM S87073).

Diagnosis. *Opopaea leica* resembles *O. antoniae* and *O. olivernashi* in colour and the large size of the eye but males of *O. leica* can be easily separated by the sternal posterior hump and hair tuft between coxae IV (Fig. 60) and by the absence of a retrolateral seam separating the bulb from cymbium. Females resemble *O. olivernashi* but can be distinguished by having their globular appendix (GAp) separated into a small posterior globular and a hoodlike anterior part, with the GAp well separated from the chitinised plate (Ch).

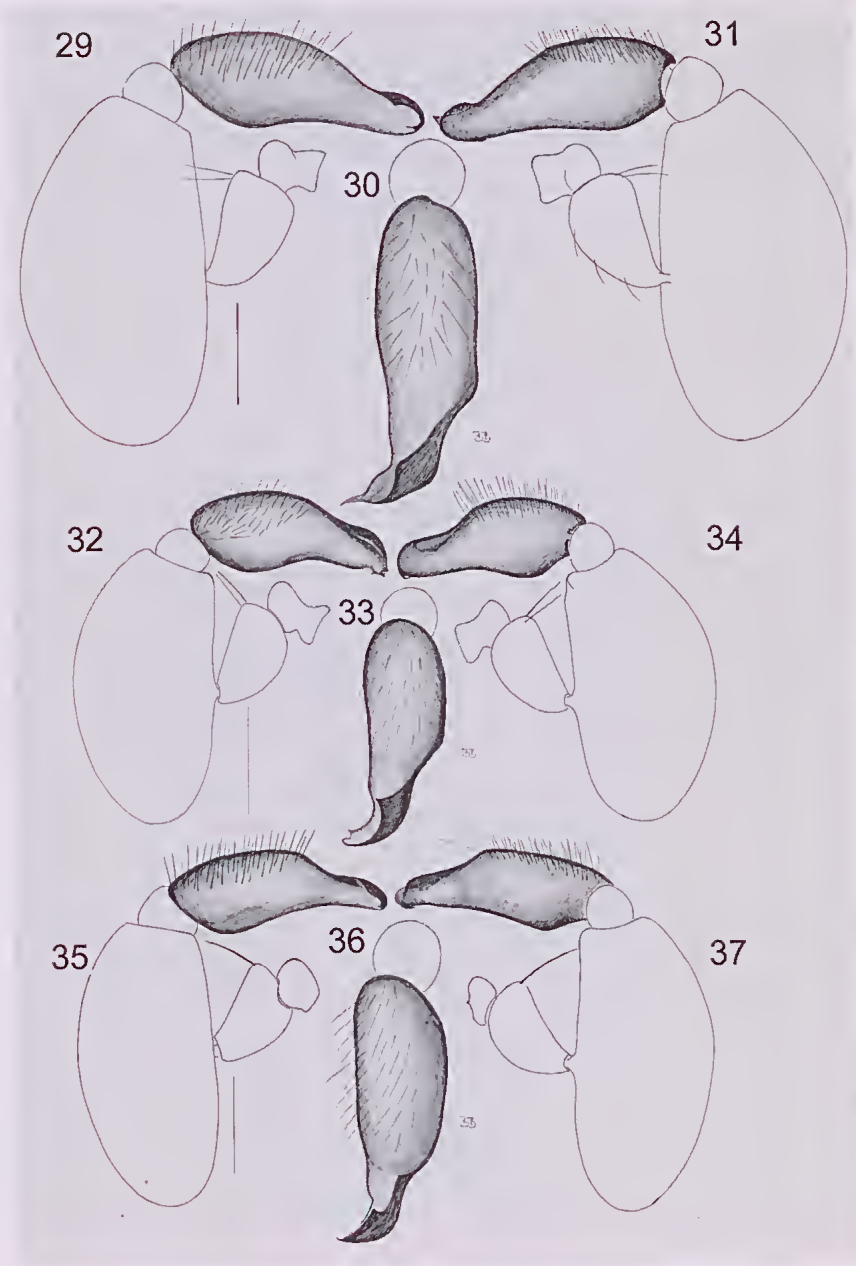
Description. *Male* (holotype, PBI_OON 23237). Total length 1.67. *Colour in alcohol.* Body and palp dark red-brown, legs yellowish. *Carapace* pars cephalica slightly elevated in lateral view, with angular posterolateral corners. *Eyes* large, ALE largest. ALE: 0.069; PME: 0.057; PLE: 0.048; eye quadrangle: 0.201; PME oval, PLE circular; ALE separated by less than their radius; ALE-PLE separated by less than ALE radius; PME touching throughout most of their length; PLE-PME separated by less than PME radius. *Sternum* furrows smooth, microsculpture absent, with posterior swelling between coxae



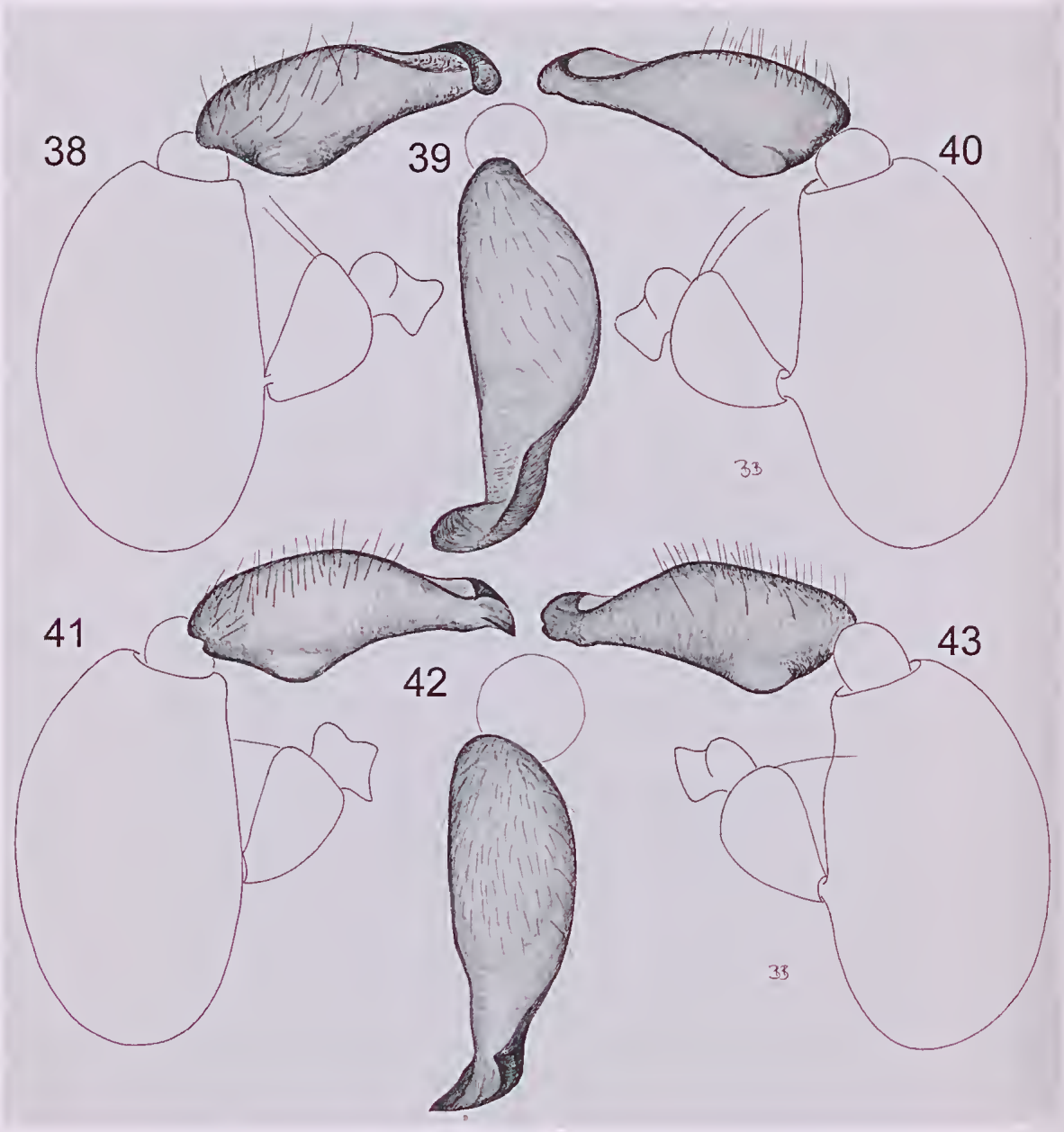
FIGS 15–19. *Opopaea antoniae* sp. nov. (PBI_OON 23360). 15-17, leg I dorsal view of tarsus (15), metatarsus (16) and tibia (17); 18, tarsal organ; 19, left palp dorsal.



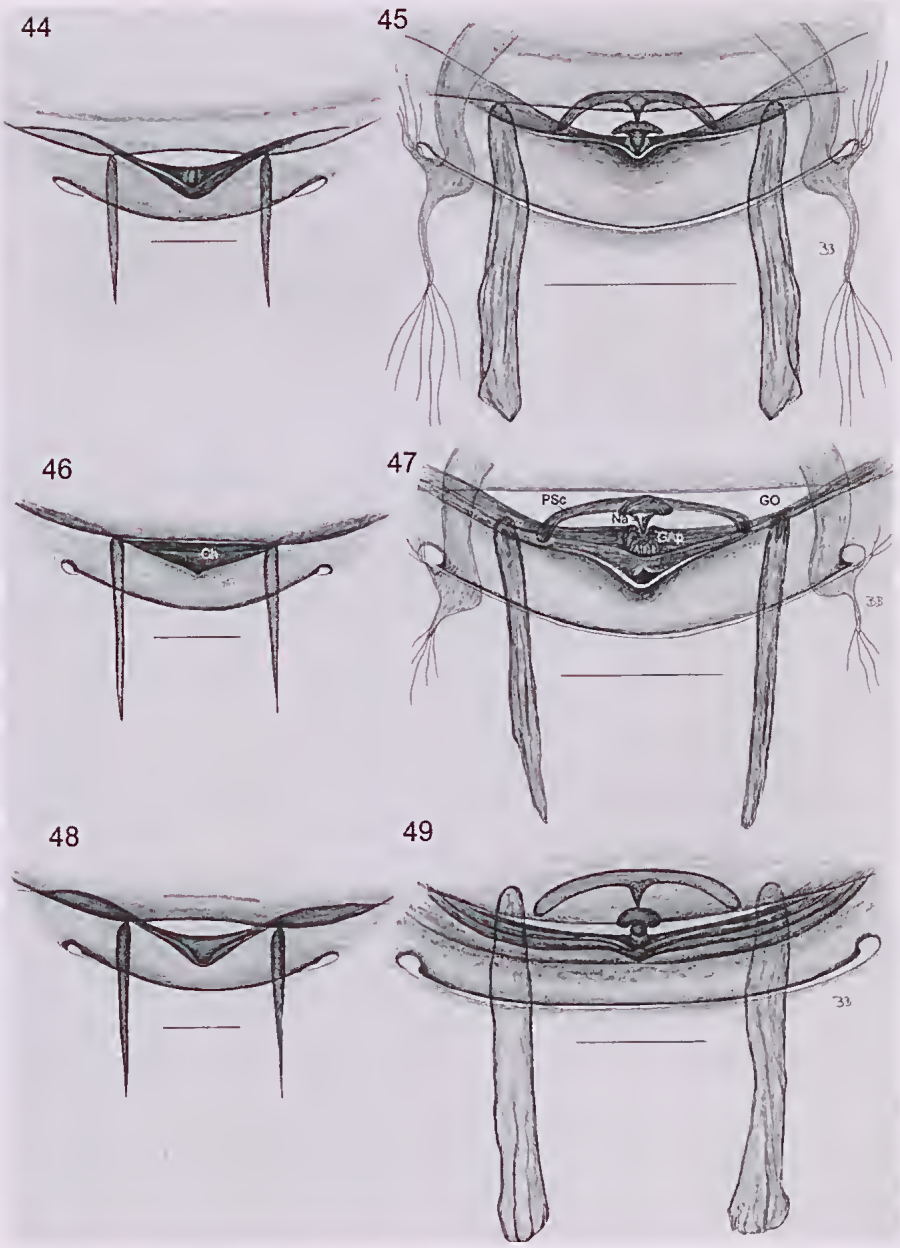
FIGS 20–28. *Opopaea* species left palp. 20, 23, 26, prolateral view; 21, 24, 27, dorsal view; 22, 25, 28, retrolateral view. 20–22, *O. olivernashi* sp. nov. (PBI_OON 23254); 23–25, *O. antoniae* sp. nov. (PBI_OON 23239); 26-28, *O. leica* sp. nov. (PBI_OON 23237). L, patella length; C, length of connection to femur. Scale bar = 0.1 mm.



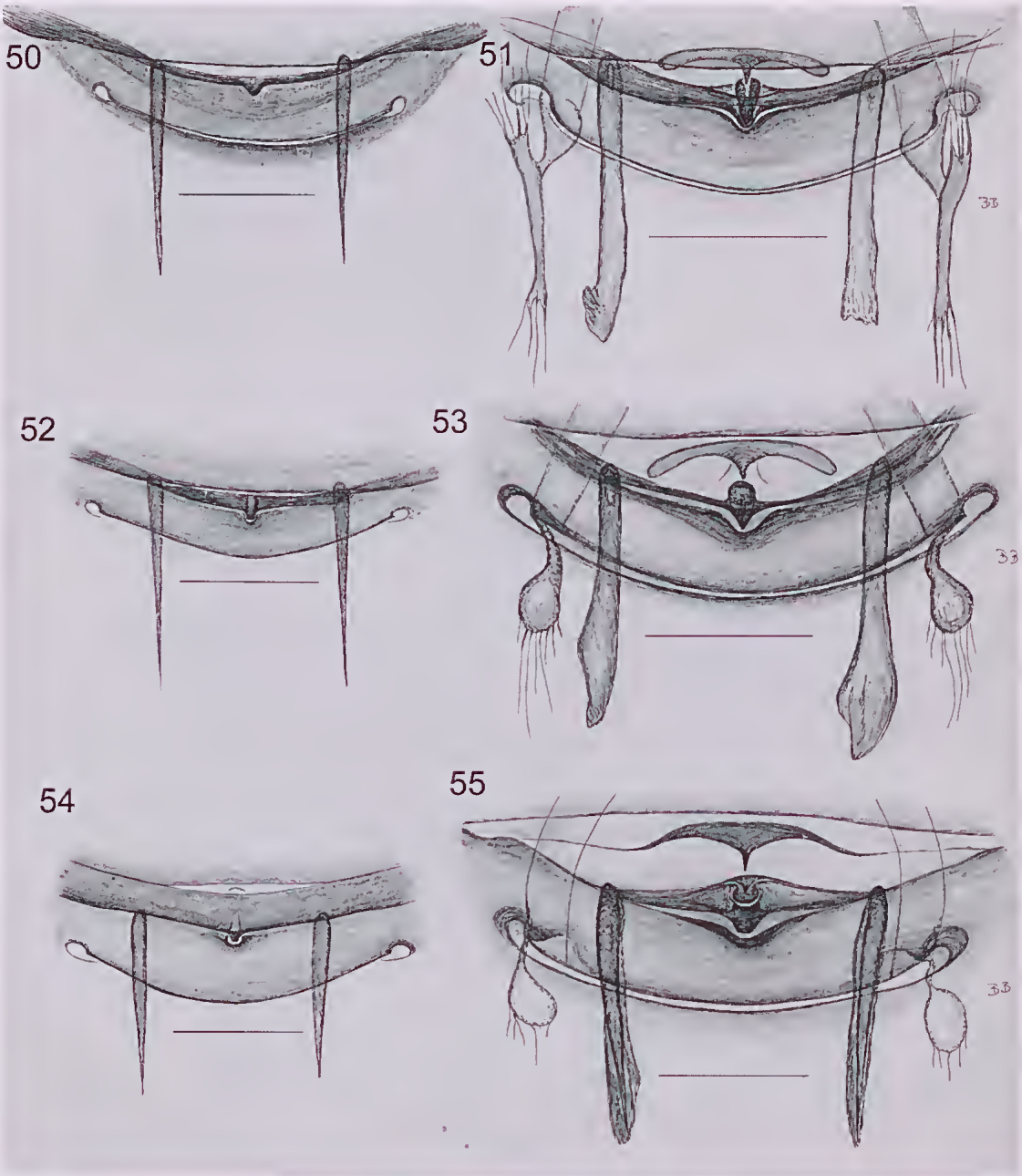
FIGS 29–37. *Opopaea* species left palp. 29, 32, 35, prolateral view; 30, 33, 36, dorsal view; 31, 34, 37, retrolateral view. 29–31, *O. jonesae* sp. nov. (PBI_OON 22746); 32–34, *O. sown* sp. nov. (PBI_OON 22751); 35–37, *O. rogerkitchingi* sp. nov. (PBI_OON 22772). Scale bars = 0.1 mm.



FIGS 38–43. *Opopaea* species left palp. 38, 41, prolateral view; 39,42, dorsal view; 40, 43, retrolateral view. 38–40, *O. yukii* sp. nov. (PBI_OON 6383); 41–43, *O. speighti* sp. nov. (PBI_OON 23256).



FIGS 44–49. *Opopaea* species epigyne. 44, 46, 48, ventral view; 45, 47, 49, dorsal view. 44-45, *O. olivernashi* sp. nov. (PBI_OON 23362); 46-47, *O. antoniae* sp. nov. (PBI_OON 23341); 48-49, *O. leica* sp. nov. (PBI_23282). Ch, chitinised area; GAp, globular appendix; GO, genital opening; Na, nail-like process; PSc, paddle-like sclerite. Scale bars = 0.1 mm.



FIGS 50–55. *Opopaea* species epigyne. 50, 52, 54, ventral view; 51, 53, 55, dorsal view. 50-51, *O. sown* sp. nov. (PBI_OON 23289); 52-53, *O. jonesae* sp. nov. (PBI_OON 23267); 54-55, *O. rogerkitchingi* sp. nov. (PBI_OON 22734). Scale bars = 0.1 mm.

IV and with hair tuft (Fig. 60). *Abdomen*: Book lung covers large, ovoid. *Palp* (26, 28): patella big, club-shaped, W/L=0.59; connection to femur C/L= 0.39; L=0.255; W=0.150; C=0.100; cymbium completely fused with bulb, no seam visible, distal end medially bent with sharp corner.

Female. (paratype, PBI_OON 23282) Total length 1.93. As in male except as noted. *Eyes* large. ALE: 0.065; PME: 0.55; PLE: 0.46; eye quadrangle: 0.199. *Genitalia* (Figs 46, 47): Chitinised area (Ch), in ventral view, a widely triangular sclerite; globular appendix (GAp) separated into a small posterior globular and an anterior hoodlike part, with the GAp well separated from the chitinised plate (Ch).

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

Opopaea olivernashi sp. nov.
(Figs 4, 20–22, 44, 45, 61, 63)

Etymology. A patronym in honour of Oliver Nash, an 8 year old boy who has been fascinated by spiders since he was 4 years old.

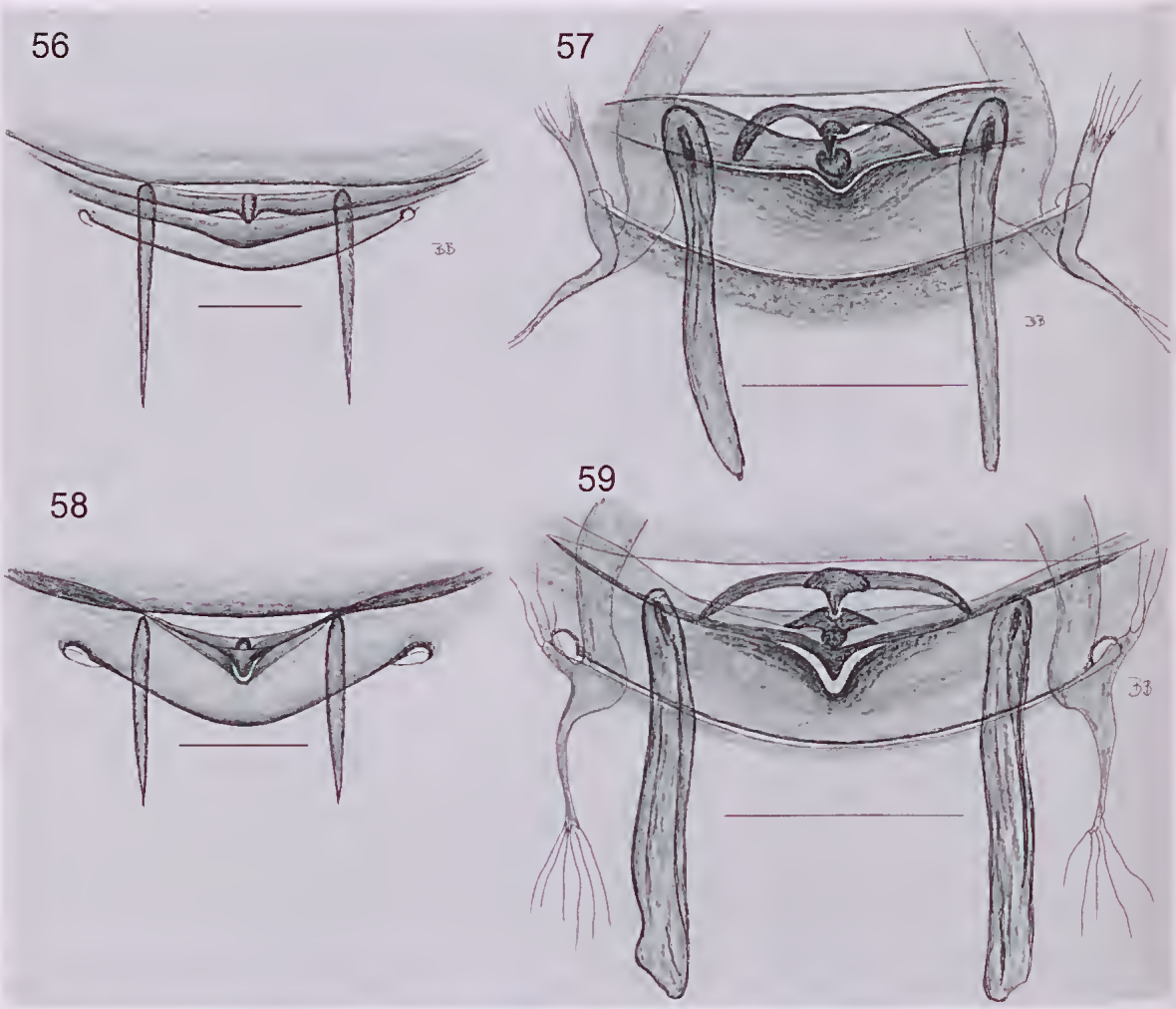
Material. Holotype ♂, Queensland, Lamington NP, 0.5 km SSE Binna Burra Lodge, 28.198°S 153.190°E, 770 m, 18 Mar 2008, SW, AN, berlesate sifted litter (PBI_OON 23254, QM S86323). PARATYPE, QUEENSLAND, 1♀, Lamington NP IBISCA, 500A, 28.35°S 153.23333°E, 560 m, 28 Jan 2008, SW, AN, litter extract (PBI_OON 23362, QM S87068). Other Material. QUEENSLAND, IBISCA 500A: 1♂, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23269, QM S86389; PBI_OON 23279, QM S86392). IBISCA 500C: 1♂, 28 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23278, QM S86388). IBISCA 500D: 6♂, 28 Jan 2008, SW, AN, litter extract (PBI_OON 23313, QM S86379, PBI_OON 23363, QM S87069). IBISCA 700C: 1♂, 20 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23286, QM S86353). IBISCA 850, 1♂, 29 Jan 2008, AN, bark spray (PBI_OON 23283, QM S86337). 1♂, Lamington NP, 0.5 km SSE Binna Burra Lodge, 28.198°S 153.190°E, 770 m, 18 Mar 2008, SW, AN, berlesate sifted litter (PBI_OON 23292, QM S86324); 1♂ same data except pyrethrum (PBI_OON 23271, QM S86362).

Other diagnosis. *Opopaea olivernashi* resembles *O. antoniae* in colour and eye size. Males of *O. olivernashi* and *O. antoniae* are the only Lamington species with a retrolateral seam between the bulb and cymbium. Males of *O. olivernashi* can be easily separated by their broad patella, the more subbasal connection to the femur (C/L = 0.37), the sternum with an anterior fold just behind labium, about ¾ of the length of the labium (Fig. 61), and the more swollen bulb. Females can be distinguished from all other *Opopaea* species by the globular appendix divided into a hood and a v-shaped extension (Fig. 45).

Description. *Male* (holotype, PBI_OON 23254). Total length 1.44. *Colour in alcohol*. Body and palpal patella dark yellow-brown, legs pale orange. *Carapace* broadly oval in dorsal view, pars cephalica slightly elevated in lateral view, with angular posterolateral corners. *Clypeus* with 4 long setae in slightly v-shaped arrangement. *Eyes* large, ALE largest; ALE: 0.077; PLE: 0.044; PME: 0.057; Eye-group width: 0.212; PME oval, PLE circular; ALE separated by less than their radius, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by less than PME radius. *Sternum* (Fig. 61) with anterior fold just behind labium, about ¾ of length of labium, and without posterior swelling between coxae IV. *Abdomen*: Book lung covers large, ovoid. Palp (Figs 22–24) patella big, club-shaped, W/L=0.63; connection to femur C/L= 0.37; L=0.208; W=0.132; C=0.077; cymbium fused with bulb but with clearly defined seam between, with distal patch of setae; bulb orange-brown.

Female. (PBI_OON 23362) Total length 1.87. As in male except as noted. *Clypeus* with 4 long setae forming in inverted v-shaped arrangement. *Eyes* large, ALE: 0.064; PME: 0.054; PLE: 0.45; eye quadrangle: 0.197. *Genitalia* (Figs 44, 45): in ventral view, chitinised area (Ch) a widely triangular plate rounded posteriorly, separated into 2 parts; in dorsal view paddle-like sclerite (PSc) with evenly bent arms; nail-like process (Na) small; globular appendix (GAp) divided into hood and v-shaped extension.

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

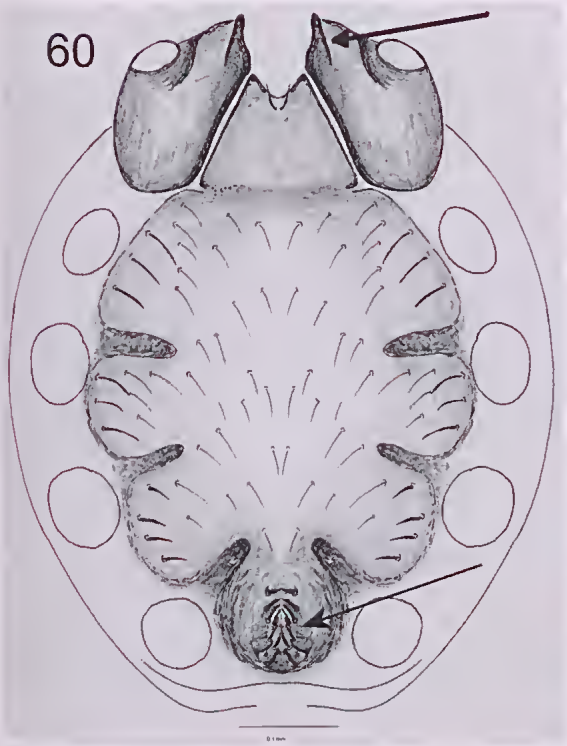


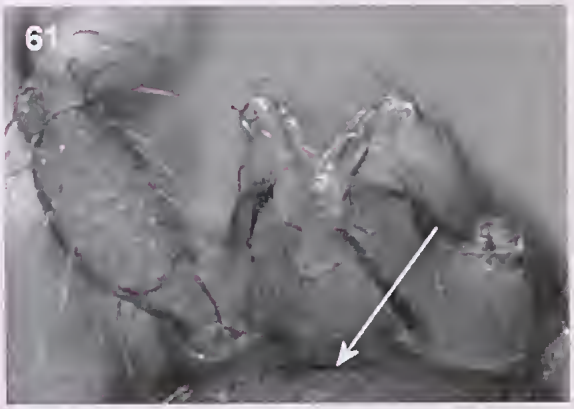
FIGS 56–59. *Opopaea* species epigyne. 56, 58, ventral view; 57, 59, dorsal view. 56-57, *O. yukii* sp. nov. (PBI_23299); 58-59, *O. speighti* sp. nov. (PBI_23295). Scale bars = 0.1 mm.

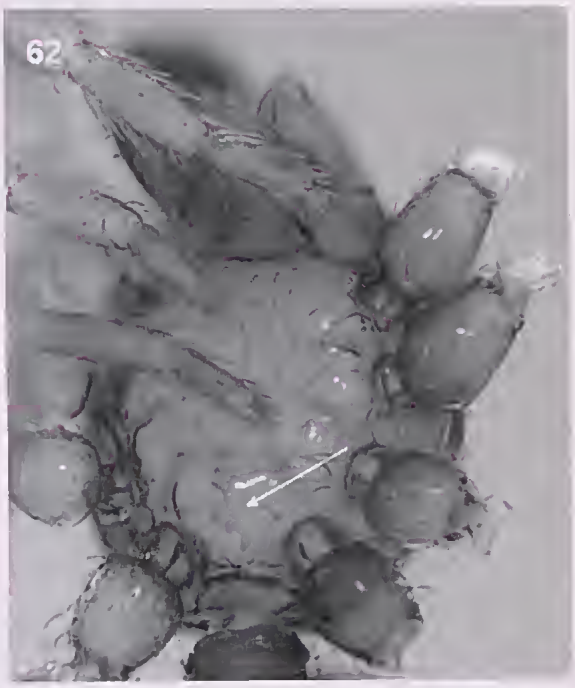
Opopaea rogerkitchingi sp. nov.
(Figs 5, 35–37, 54, 55, 63)

Etymology. A patronym in honour of Prof. Roger Kitching from Griffith University, who founded the IBISCA-Queensland Project (Investigating the Biodiversity of Soil and Canopy Arthropods).

Material. Holotype ♂, Queensland, Lamington NP, IBISCA, 1100C, 28.260°S 153.167°E, 1106 m, 16 Mar 2007, CB, night hand coll. (PBI_OON 22772, QM S79897). PARATYPE, QUEENSLAND, 1♀, Lamington NP, IBISCA 1100D, 28.262°S 153.170°E, 1140 m, 5–7 Oct 2006, JB, KS, pitfall (PBI_OON 22734, QM S81149). OTHER MATERIAL, QUEENSLAND, IBISCA 700C: 2♀, 11–20 Oct 2006, KS, pitfall (PBI_OON 22735, QM S81066). IBISCA 900A: 1♀, 11–20 Mar 2007, DP, KS, pitfall (PBI_OON 23326, QM S86398). IBISCA 900C: 1♀, 11–20 Mar 2007, DP, KS, pitfall (PBI_OON 23324, QM S86396); 1♀, 24 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23325, QM S86399); 1♂, 28 Mar–2 Apr 2007, GM, fungus pitfall (PBI_OON







FIGS 60–62. *Opopaea* species, male sternum ventral. 60, *O. leica* sp. nov. (PBI_23237), top arrow pointing to tooth-like projection at anteromedian tip of endite, bottom arrow pointing to posterior hump and hair tuft between coxae IV; 61, *O. olivernashi* sp. nov. (PBI_23279), arrow pointing to anterior fold just behind labium; 62: *O. jonesae* sp. nov. (PBI_22751), arrow pointing to posterior swelling with longitudinal row of setae.

23242, QM S86314). IBISCA 900D: 1♂, 5–8 Oct 2006, KS, BB, pitfall (PBI_OON 22757, QM S81141). IBISCA 1100A: 1♂, 1♀, 11–20 Oct 2006, S. Maunsell, pitfall (PBI_OON 22752, QM S81060); 2♂, 11–20 Mar 2007, DP, K. Staunton, pitfall (PBI_OON 23294, QM S86361); 1♀, 27 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23329, QM S86397). IBISCA 1100B: 1♂, 27 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23291, QM S86394), 2♀, same data (PBI_OON 23290, QM S86365). IBISCA 1100C: 1♂, 2–5 Oct 2006, KS, B. Taylor, pitfall (PBI_OON 22771, QM S81016); 1♀, 7–11 Oct 2006, KS, pitfall (PBI_OON 22730, QM S81132); 1♂, 11–20 Mar 2007, DP, KS, pitfall (PBI_OON 23297, QM S86359). IBISCA 1100D: 1♂, 5–7 Oct 2006, JB, KS, pitfall (PBI_OON 22753, QM S81085). 1♀, Lamington Plateau, 28.317°S 153.067°E, 31 Oct 1982, J. Grimshaw, litter (PBI_OON 7215, QM S78257).

Diagnosis. *Opopaea rogerkitchingi* resembles *O. jonesae* in colour and both species have small eyes that are equal in size. Males of *O. rogerkitchingi* and *O. jonesae* also share a slim bulb, and a palpal patella with a median connection to the femur (C/L=0.52). Males of *O. rogerkitchingi* can be easily separated by the centrally directed sternal setae between coxae IV and the distal part of bulb which has a medially bent, sharp tip (Fig. 36). Females of *O. rogerkitchingi* can be distinguished from those of *O. jonesae* by the broad chitinised area near the genital opening (Fig. 54).

Description. *Male* (holotype, PBI_OON 22772). Total length 1.52. *Colour in alcohol.* Body yellow-brown, legs pale orange, palpal patella reddish brown. *Carapace* pars cephalica flat in lateral view, with angular posterolateral corners. *Eyes* small, subequal; ALE: 0.034; PME: 0.030; PLE: 0.021; eye quadrangle: 0.130, PME oval, PLE circular; ALE separated by more than their diameter, ALE-PLE separated by less than ALE radius, PME touching for less than half their length, PLE-PME separated by PME radius to PME diameter. *Sternum* posterior part of sternum between coxae IV bulging, with setae directed centrally. *Abdomen*: book lung covers large, ovoid. Palp (Figs 35–37): patella big, club-shaped, W/L=0.47; connection to femur C/L=0.52; L=0.330; W=0.156; C=0.173; cymbium completely fused with bulb, no seam visible, distally with medially bent, sharp tip. *Female* (paratype, PBI_OON 22734). Total length 1.62. As in male except as noted. *Eyes* small. ALE: 0.034; PME: 0.035; PLE: 0.027; eye quadrangle: 1.41. *Genitalia* (Figs 54, 55): chitinised area (Ch) a broad band in ventral view; in dorsal view, paddle-like sclerite (PSc) with evenly bent arms; nail-like process (Na) not separated; globular appendix (GAp) globular with a small globular anterior part and a squared posterior part.

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

Opopaea sown sp. nov.
(Figs 6, 32–34, 50, 51, 63)

Etymology. A patronym in honour of Anne Jones' company named "Save Our Waterways Now Inc" (also known as SOWN) and her support for this taxonomic work.

Material. Holotype ♂, Queensland, Lamington NP, IBISCA, 300B, 28.155°S 153.139°E, 282 m, 6 Oct 2006, BB, hand coll. (PBI_OON 22746, QM S75881). OTHER MATERIAL, QUEENSLAND, IBISCA 300B: 1♂, 13–22 Mar 2007, DP, KS, pitfall (PBI_OON 23250, QM S86321); 1♀, 25 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23287, QM S86349). IBISCA 300C: 1♂, 12–21 Feb 2007, KS, pitfall (PBI_OON 22710, QM S76076); 1♂, 25 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23288, QM S86345), 2♀, (PBI_OON 23285 QM S86348, PBI_OON 23288, QM S86345). IBISCA 300D: 1♀, 1♂, 25 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23289, QM 86347).

Diagnosis. *Opopaea sown* is the smallest *Opopaea* species from Lamington National Park. It resembles *O. rogerkitchingi* and *O. jonesae* in colour and in having small equal-sized eyes. Males of *O. sown*, *O. rogerkitchingi* and *O. jonesae* all have a slim bulb and a palpal patella with a median connection to the femur (C/L=0.47 in *O. sown*). Males of *O. sown* can be easily separated from both the other species by the sternum, which has evenly scattered setae (as in Fig. 11) and is unswollen between coxae IV, and by the bifurcate distal part of the bulb (Fig. 33). Females of *O. sown* can be distinguished from those of *O. jonesae* by having a globular appendix (GAp) that lacks a hood but has a long, wedge-like extension (Fig. 51).

Description. *Male* (holotype, PBI_OON 22746). Total length 1.31. *Colour in alcohol.* Body and legs pale orange, palpal patella orange-brown. *Carapace* broadly oval in dorsal view, pars cephalica flat in lateral view, with angular posterolateral corners. *Eyes* small, subequal; ALE: 0.041; PME: 0.035; PLE: 0.023; eye quadrangle: 0.143; PME oval; PLE circular; ALE separated by their radius to diameter, ALE-PLE separated by less than ALE radius, PME touching for less

than half their length, PLE-PME separated by less than PME radius. *Sternum* without posterior hump between coxae IV; setae sparse, evenly scattered. *Abdomen*, book lung covers large, ovoid. Palp (Figs 32–34) patella big, club-shaped, W/L=0.53; connection to femur C/L=0.47; L=0.265; W=0.140; C=0.125; cymbium completely fused with bulb, no seam visible, bulb with bifurcate, medially bent distal part (Fig. 33).

Female. (PBI_OON 23289) Total length 1.45. As in male except as noted. *Eyes* small subequal; ALE: 0.046; PLE: 0.025; PME: 0.036; eye quadrangle: 0.136. *Genitalia* (Figs 50, 51): narrow, widely triangular chitinised area (Ch) with small median triangle in ventral view; in dorsal view, paddle-like sclerite (PSc) with evenly thick, nearly straight arms; nail-like process (Na) relatively small, well separated; globular appendix (GAp) globular with long triangular wedge-like extension, embedded in chitinised area.

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

Opopaea speighti sp. nov.
(Figs 7, 41–43, 58, 59, 63)

Etymology. A patronym in honour of David Speight who loves little creatures. He is the son of Dr Shelia Bryan who supported spider taxonomy through the Queensland Museum.

Material. Holotype ♂, Queensland, Lamington NP, IBISCA, 1000, 28.247°S 153.149°E, 995 m, 10 Feb 2008, CB, AN, leaf litter extract (PBI_OON 23256, QM S86363). PARATYPE, QUEENSAND, 1♀, Lamington NP, IBISCA, 1000, 28.247°S 153.149°E, 995 m, 10 Feb 2008, CB, AN, leaf litter extract (PBI_OON 23295, QM S86364). OTHER MATERIAL, QUEENSLAND, IBISCA 900A: 1♀, 5–8 Oct 2006, KS, pitfall (PBI_OON 22754, QM S81024); 1♂, 18 Jan 2008, AN, leaf litter extract (PBI_OON 23321, QM S86404). IBISCA 900C: 1♂, 24 Jan 2008, SW, AN, leaf litter extract (PBI_OON 23327, QM S86405).

Diagnosis. *Opopaea speighti* resembles *O. leica* in having a completely fused bulb and cymbium, and a triangular, medially bent distal part of the bulb (Figs 27, 42). Males of *O. speighti* can be easily separated by their flat sternum which lacks any posterior swelling between coxae IV. Females of *O. speighti* can be distinguished from those of all other *Opopaea* species by the genitalia which have a narrow, triangular, posteriorly directed extension of the chitinised area in ventral view (Fig. 58) and the globular appendix divided into a widely triangular, hood-shaped anterior part and a small, globular posterior extension that is not embedded in the chitinised area (Fig. 59).

Description. *Male* (holotype, PBI_OON 23256). Total length 1.50. *Colour in alcohol*. Body yellow-brown, legs pale orange, palpal patella reddish brown. *Carapace* broadly oval in dorsal view, pars cephalica slightly elevated in lateral view, with angular posterolateral corners. *Clypeus* with with 4 long setae in slightly v-shaped position and 2 additional setae bending backwards. *Eyes* large but PME largest; ALE: 0.048; PLE: 0.038; PME: 0.050; eye-group width: 0.186 (mm), PME largest, PME oval, PLE circular; ALE separated by their radius to diameter, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by less than PME radius. *Sternum* evenly covered with posteriorly directed setae. *Abdomen*, book lung covers large, ovoid. *Palp* (Figs 41–43) patella big, club-shaped, W/L=0.58; connection to femur C/L=0.45. L=0.310; W=0.181; C=0.139; cymbium completely fused with bulb, distal end long triangular and bent medially.

Female. (paratype, PBI_OON 23295) Total length 1.97. As in male except as noted. *Eyes* large, ALE largest; ALE: 0.070; PLE: 0.053; PME: 0.058; eye quadrangle: 0.217. *Genitalia* (Figs 58, 59): narrow triangular chitinised area (Ch) with long, narrow, posteriorly directed triangular extension in ventral view; in dorsal view paddle-like sclerite (PSc) with wide, evenly bent arms; nail-like process (Na) large, well-separated; globular appendix (GAp) with wide anterior triangular hood and small globular posterior extension, not embedded in chitinised area.

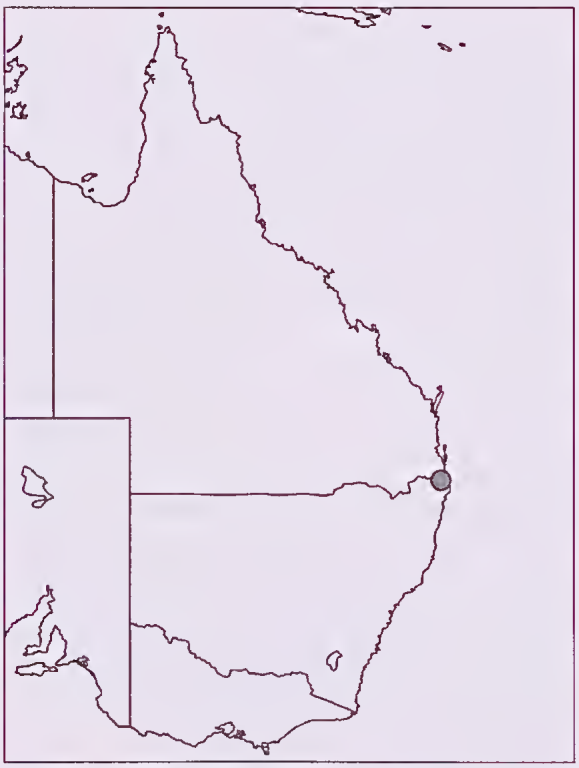


FIG. 63. Map of eastern Australia indicating the location of Lamington National Park and the eight *Opopaea* species described herein.

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

Opopaea yukii sp. nov.
(Figs 8, 9, 38–40, 56, 57)

Etymology. Named for Yuki Nakamura, the son of Aki Nakamura, from the Queensland Museum, who collected many of the specimens examined in this study.

Material. Holotype ♂, Queensland, Lamington NP, IBISCA, 700D, 28.204°S 153.129°E, 748 m, 12 Mar 2007, GT, bark spray (PBI_OON 6383, QM S75399). PARATYPE, QUEENSLAND, 1♀, Lamington NP, IBISCA, 700D, 28.204°S 153.129°E, 748 m, 12 Mar 2007, GT, bark spray (PBI_OON 23357, QM S84084). OTHER MATERIAL, QUEENSLAND, IBISCA 300A: 3♀, 1♂, 8 Mar 2007, GT, bark spray (PBI_OON 6373, QM S75389; PBI_OON 6377, QM S75393); 1♀, 9–11 Oct 2006, KS, pitfall (PBI_OON 22728, QM S81051); 8♂, 16 Oct 2006, CB, bark spray (PBI_OON 22665, QM S79843, PBI_OON 22674, QM S79837), 5♀ (PBI_OON 22665, QM S79843, PBI_OON 22674, QM S79837); 1♀, 2♂, 25 Jan 2008, SW, bark spray (PBI_OON 23304, QM S86341). IBISCA 300B: 5♀, 1♂, 16 Oct 2006, CB, bark spray (PBI_OON 22677, QM S79842; PBI_OON 22693, QM S79841); 1♀,14–23 Jan 2007, KS, pitfall (PBI_OON 23244, QM S86313); 2♀, 1♂, 9 Mar 2007, GT, AM, bark spray (PBI_OON 6389, QM S75406); 2♀, 1♂, 25 Jan 2008, SW, bark spray (PBI_OON 23299, QM S86350); 3♀, 3♂, 25 Jan 2008, AN, bark spray (PBI_OON 23255, QM S86329). IBISCA 300C: 1♂, 21 Oct 2006, CB, bark spray (PBI_OON 22688, QM S79836); 2♂, 21 Oct 2006, CB, bark spray (PBI_OON 22676, QM S79822); 1♂, 27 Oct 2006, CB, night hand coll. (PBI_OON 22719, QM S79896); 4♀, 1♂, 25 Jan 2008, SW, bark spray (PBI_OON 23302, QM S86326); 1♀, 2♂, 25 Jan 2008, AN, bark spray (PBI_OON 23300, QM S86342. IBISCA 300D: 1♂, 2–6 Oct 2006, BB, KS, pitfall (PBI_OON 22712, QM S79898); 1♂, 6–9 Oct 2006, KS, pitfall (PBI_OON 22717, QM S81097); 3♂,16 Oct 2006, CB, bark spray (PBI_OON 22678, QM S79840, PBI_OON 22690, QM S79828); 8♂, 9 Mar 2007, GT, AM, bark spray (PBI_OON 6387, QM S75402; PBI_OON 6397, QM S75414); 2♀, 25 Jan 2008, SW, bark spray (PBI_OON 23301, QM S86344); 1♀, 3♂, 25 Jan 2008, AN, bark spray (PBI_OON 23303, QM S86351). IBISCA 500A: 7♀, 2♂, 14 Mar 2007, GT, bark spray (PBI_OON 6374, QM S75390); 1♀, 1♂, 19 Mar 2007, SW, bark spray (PBI_OON 6412, QM S75429); 1♀, 28 Jan 2008, SW, bark spray (PBI_OON 23328, QM, S86402). IBISCA 500B: 1♀, 28 Jan 2008, AN, bark spray (PBI_OON 23298, QM S86377). IBISCA 500C: 1♀, 28 Jan 2008, SW, bark spray (PBI_OON 23296, QM S86378). IBISCA 500D: 5♀, 28 Jan 2008, AN, bark spray (PBI_OON 23323, QM S86403). IBISCA 700A: 1♀, 10 Mar 2007, GT, bark spray (PBI_OON 6376, QM S75392); 3♂, 8♀, 10 Mar 2007, GT, bark spray (PBI_OON 6372, QM S75388); 2♀, 20 Oct 2006, CB, bark spray (PBI_OON 22687, QM S79833); 3♂, 10 Mar 2007, GT, bark spray (PBI_OON 6381, QM S75397); 1♂, 26 Sep 2008, GM, FT, bark spray (PBI_OON 23359, QM S87070); 2♀, (PBI_OON 00023359, QM S87070). IBISCA 700B: 3♀, 20 Oct 2006, CB, bark spray (PBI_OON 22682, QM S79821); 2♂, 20 Oct 2006, CB, bark spray (PBI_OON 22671, QM S79827); 3♀, (PBI_OON 22671, QM S79827); 1♂, 28 Oct 2006, CB, night hand coll. (PBI_OON 22747, QM S75879). IBISCA 700D: 1♂, 19 Oct 2006, CB, bark spray (PBI_OON 22667, QM S79818); 2♂, 12 Mar 2007, GT, AM, bark spray (PBI_OON 6406, QM S75423); 1♂, 20 Jan 2008, AN, bark spray (PBI_OON 23252, QM S86328). IBISCA 900D: 1♂, 8 Mar 2007, GT, bark spray (PBI_OON

6413, Q M

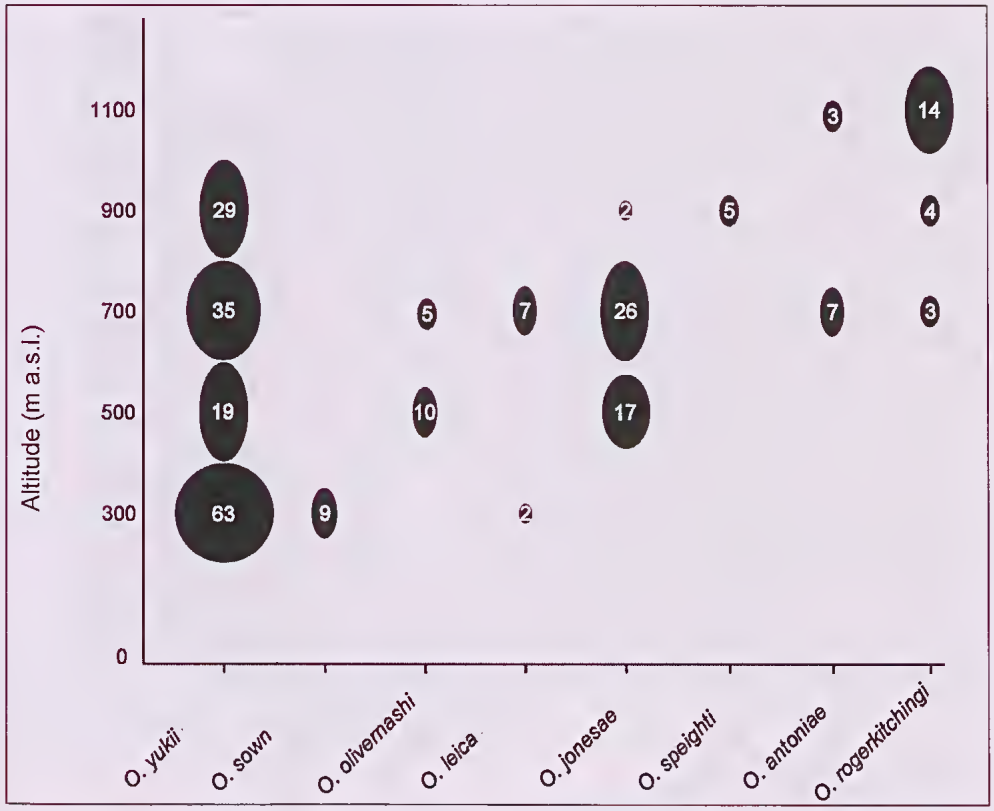


FIG. 64. Altitudinal distribution of the eight *Opopaea* species of the Lamington National Park based on a total of 255 specimens collected during the IBISCA-Queensland project. Oval lines indicate the small-eyed litter species (*O. sown* sp. nov., *O. jonesae* sp. nov., *O. rogerkitchingi* sp. nov.).

S75431), 1♀, (PBI_OON 6380, QM S75395); 1♂, 9 Mar 2007, GT, bark spray (PBI_OON 6408, QM S75426); 6♀, 10 Mar 2007, GT, bark spray (PBI_OON 6386, QM S75403); 2♀, 19 Mar 2007, SW, bark spray (PBI_OON 6410, QM S75428). IBISCA 1100A: 1♂, 25 Oct 2006, CB, bark spray (PBI_OON 23238, QM S86312).

Diagnosis. Males and females of *O. yukii* can be easily separated from all other *Opopaea* species from Lamington National Park by their flat bodies and long oval abdomens (Figs 8, 9). The male sternum has no posterior swelling between coxae IV and the distal end of the palpal bulb is long, medially bent and scoop-shaped. Females can be distinguished from those of all other *Opopaea* species by having the chitinised area a narrow band with a small sinuous posterior extension (Fig. 56) in ventral view and the globular appendix not divided but small, globular and embedded in the chitinised area (Fig. 57).

Description. *Male* (holotype, PBI_OON_6383). Total length 1.65. *Colour in alcohol.* Body orange-brown, legs yellow, palpal patella reddish brown. *Carapace* flat in lateral view, with angular posterolateral corners. *Eyes* large, ALE largest; ALE: 0.076; PLE: 0.048; PME: 0.052; eye group width=0.212, PME circular, PLE oval; posterior

eye row straight from front; ALE separated by less than their radius, ALE-PLE touching, PME touching throughout most of their length, PLE-PME touching. *Sternum* without posterior swelling; setae sparse, evenly scattered. *Abdomen*, book lung covers large, ovoid. Palp (Figs 38–40) patella club-shaped, W/L=0.55; connection to femur C/L=0.46. L=0.330; W=0.180; C=0.15; cymbium completely fused with bulb.

Female. (PBI_OON 23357) Total length 1.80. As in male except as noted. *Eyes* large; ALE: 0.075; PLE: 0.044; PME: 0.051; eye quadrangle 0.211. *Genitalia* (Figs 56, 57): Chitinised area a narrow band with small sinuous posterior extension in ventral view (Fig. 56); in dorsal view paddle-like sclerite (PSc) with wide, evenly bent arms; nail-like process (Na) small well-separated; globular appendix (GAp) not divided but small, globular, embedded in chitinised area (Fig. 57).

Distribution. Only known from the southeast corner of Queensland (Fig. 63).

ACKNOWLEDGMENTS

This paper is dedicated to the people and institutions that support taxonomic science with their encouragement. This paper would not have been completed without the efforts of Roger Kitching who founded the IBISCA-Queensland project. I am deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. Cash support for the IBISCA-QLD project was also received from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. This taxonomic work was also supported by the National Science Foundation's PBI (Planetary Biodiversity Inventory) program through grant DEB-0613754. Thanks to Owen Seeman and Wendy Hebron (Queensland Museum, Brisbane) for the loan of the material and their great support of the work. I particularly would like to thank members of the IBISCA-Queensland team, Chris Burwell, Geoff Monteith, Aki Nakamura, David Putland, Kyran Staunton, Geoff Thompson, Federica Turco and Susan Wright from the Queensland Museum and Griffith University who collected the *Opopaea* specimens here examined. Special thanks to Robert Raven, for his great support with the SEM work using the Hitachi S530. I also would like to thank my daughters; Johanna, who assisted passionately in databasing and developing the distribution chart for the *Opopaea* specimens, and Ursula for being patient.

LITERATURE CITED

Baehr, B.C. 2008. Revision of the Australian antspider genus *Habronestes* L. Koch, 1872 (Araneae: Zodariidae): III The *Habronestes macedonesis*-group in Queensland and New South Wales. *Memoirs of the Queensland Museum* **52**: 25-47.

Baehr, B.C. & Smith, H.M. 2008. Three new species of the Australian orsolobid spider genus *Hickmanolobus* (Araneae: Orsolobidae). *Records of the Western Australian Museum* **24**: 325-336.

Baehr, B.C., Harvey, M.S. & Smith, H.M. 2010. The new endemic Australian goblin spider genus *Cavisternum* (Araneae: Oonopidae). *American Museum Novitates* **3684**: 1-40.

Burger, M. 2010. Complex female genitalia indicate sperm dumping in armored goblin spiders (Arachnida, Araneae, Oonopidae). *Zoology* **113**: 19-32.

Burwell, C.J. & Nakamura, A. 2011. Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum - Nature* 55(2): 391-411.

Harvey, M.S. 1987. *Grymeus*, a new genus of pouched oonopid spider from Australia (Chelicerata: Araneae). *Memoirs of the Museum of Victoria* **48**: 123-130.

2002. Short-range endemism in the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics* **16**: 555-570.

Harvey, M.S. & Edward, K.L. 2007. Three new species of cavernicolous goblin spiders (Araneae, Oonopidae) from Australia. *Records of the Western Australian Museum* **24**: 9-17.

Hickman, V.V. 1932. Studies in Tasmanian spiders. Part V (The Oonopidae). *Papers and Proceedings of the Royal Society of Tasmania* **1931**: 20–31.

1950. Araneae from Reevesby Island, South Australia. *Proceedings of the Royal Society Victoria (N.S.)* **60**: 1-16.

1979. Some Tasmanian spiders of the families Oonopidae, Anapidae and Mysmenidae. *Papers and Proceedings of the Royal Society of Tasmania* **113**: 53-79.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along altitudinal gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum - Nature* **55**(2): 235-250.

Koch, L. 1873. *Die Arachniden Australiens, nach der Natur beschrieben und abgebildet.* Nürnberg: Bauer und Raspe 1: 369-472.

Ott, R. & Harvey, M.S 2008a. A new species of *Xestaspis* (Araneae: Oonopidae) from the Pilbara region of Western Australia. *Records of the Western Australian Museum* **24**: 337-342.

2008 b. A new species of *Pelicinus* from Barrow Island, Western Australia (Araneae: Oonopidae). *Arthropoda Selecta* **17**(1-2): 81-85.

Platnick, N.I. & Baehr, B. 2006. A revision of the Australasian ground spiders of the family Prodidomidae (Araneae: Gnaphosoidea). *Bulletin of the American Museum of Natural History* **298**: 1-287.

Platnick, N.I. 2009. *The world spider catalog, version 9.5.* American Museum of Natural History, New York. http://research.amnh.org/entomology/spiders/catalog/index.html

Platnick, N. I. & Dupérré, N. 2009. The goblin spider genera *Opopaea* and *Epectris* (Araneae, Oonopidae) in the New World. *Bulletin of the American Museum of Natural History* **3649**: 1-43.

Rainbow, W.J. 1920. Arachnida from Lord Howe and Norfolk Islands. *Records of the South Australian Museum* **1**: 229-272.

Raven, R.J. & Stumkat, K.S. 2005. Revisions of Australian ground-hunting spiders: II. Zoropsidae (Lycosoidea: Araneae). *Memoirs of the Queensland Museum* 50: 347-423.

Rix, M.G. 2006. Systematics of the Australasian spider family Pararchaeidae (Arachnida: Araneae). *Invertebrate Systematics* **20**: 203-254.

Simon, E. 1908. Araneae. 1re partie. *In* W. Michaelsen & R. Hartmeyer (editors), *Die Fauna Südwest-Australiens* **1**: 359-446. Jena: Gustav Fischer.

Tempelton, R. 1835. On the spiders of the genus *Dysdera* Latr. with the description of a new allied genus. *Zoological Journal* 5: 400-408.

Orsolobidae (Araneae) of the IBISCA-Queensland Project at Lamington National Park, Australia

Barbara C. BAEHR

Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia. Email: barbara.baehr@qm.qld.gov.au

CSER, School of Environmental and Life Sciences, University of Newcastle, Callaghan NSW 2308, Australia.

Robert J. RAVEN

Wendy HEBRON

Queensland Museum, PO Box 3300, South Brisbane Qld 4101, Australia. Email: robert.raven@qm.qld.gov.au

Citation: Baehr, B.C., Raven, R.J. & Hebron, W. 2011 12 20: Orsolobidae (Araneae) of the IBISCA-Queensland Project at Lamington National Park, Australia. *Memoirs of the Queensland Museum — Nature* 55(2) 439-449. Brisbane. ISSN 0079-8835.

ABSTRACT

Five species of the endemic Australian spider family Orsolobidae are recorded from the IBISCA-Queensland Project, a survey of invertebrates along an altitudinal gradient within continuous rainforest at Lamington National Park, Queensland, Australia. They comprise two species of *Hickmanolobus* and three species of *Tasmanoonops*, including the newly described *Hickmanolobus nimorakiotakisi* sp. nov. and *Tasmanoonops rogerkitchingi* sp. nov. Also recorded are *Tasmanoonops parvus* Forster & Platnick, of which the male is described for the first time, *Tasmanoonops complexus* Forster & Platnick and *Hickmanolobus ibisca* Baehr and Smith. Within Lamington National Park all five species have been collected only above around 750 m a.s.l. and consequently the Orsolobidae are recommended for inclusion in programs to monitor the impacts of climate change.

❐ *Orsolobidae, Arachnida, Araneae, IBISCA, Australia, new species, systematics, taxonomy, climate change.*

Orsolobids are small (body length about 4-5 mm), pallid spiders that are usually found on the forest floor or on bark in rainforests. All Australian orsolobids have a soft abdomen, whereas many species of goblin spiders, in the closely related and often sympatric family Oonopidae, have sclerotised abdominal scutes. The diagnostic feature of the Orsolobidae is the tarsal organ (found distally on the pedal tarsi) which has a specific structure for each species, but which can only be seen by placing one of the spider's legs into a scanning electron microscope.

Forster & Platnick (1985), revised the Orsolobidae and reported these spiders only in Australia, New Zealand and Chile. Since then, they have been described from South Africa (Griswold & Platnick 1987), Brazil and the Falkland Islands (Platnick & Brescovit 1994; Platnick 2011). Now with 182 described species in 28 genera, the Orsolobidae are an important component of the forest litter fauna of the southern hemisphere (Baehr & Smith 2008; Forster & Forster 1999; Hickman 1979). They are putatively a classical Gondwanan group and have hot spots of diversity in Australia and

New Zealand. To date, four genera are known from Australia but only two occur along the eastern seaboard. *Austrolobus* Forster & Platnick, 1985 is known only from Western Australia and *Cornifalx* Hickman, 1979 has been found only in Tasmania. The most common Australian genus, *Tasmanoonops* Hickman, 1930, now with 31 species, occurs mainly in the forests of Tasmania, New South Wales and Queensland, and just two species are recorded from Western Australia. *Hickmanolobus* Forster & Platnick, 1985 was originally known only from a single described species from Tasmania, *H. mollipes* Hickman, although Forster & Platnick (1985) noted an undescribed species from Queensland. Baehr & Smith (2008) subsequently described three new *Hickmanolobus* species from New South Wales and Queensland. One of these, *H. ibisca* Baehr & Smith, was collected in the IBISCA-Queensland survey (see Kitching *et al.* 2011) and initially tentatively identified by Raven as an "oonopid". To the rich complement of spiders at Lamington National Park, a further new species of *Hickmanolobus* as well as a second new species of *Tasmanoonops* are here described.

MATERIAL AND METHODS

Specimens were examined using a LEICA MZ16A microscope. Photomicrographic images were produced using a Leica DFC 500 and the software program AutoMontage LAS V3.7. Descriptions were generated with the aid of the PBI descriptive goblin spider database and shortened where possible. All measurements are in millimetres. Abbreviations: AM, Australian Museum, Sydney; ALE, anterior lateral eyes; IBISCA, Investigating the Biodiversity of Soil and Canopy Arthropods; NP, National Park; QM, Queensland Museum; PBI, Planetary Biodiversity Inventory; PLE, posterior lateral eyes; PME, posterior median eyes.

SYSTEMATICS

Family Orsolobidae Cooke, 1965

Genus *Hickmanolobus* Forster & Platnick, 1985

Type species. *Oonopinus mollipes* Hickman, 1932 by original designation.

Diagnosis and description. See Baehr & Smith (2008). The species description below mentions only differences from this generic description.

Species. *H. ibisca* Baehr & Smith, 2008; *H. jojo* Baehr & Smith, 2008; *H. linnaei* Baehr & Smith, 2008; *H. mollipes* (Hickman, 1932); *H. nimorakiotakisi* sp. nov.

Distribution. All species, except *H. mollipes* from Tasmania, are either from south-east Queensland or adjacent areas of north-eastern New South Wales.

KEY TO SPECIES OF *HICKMANOLOBUS* FROM QUEENSLAND AND NEW SOUTH WALES

1. Males 2
– Females (unknown for *H. jojo* and *H. nimorakiotakisi*) 6

2. Palpal embolus long, spiniform (Fig. 25) . . 3
– Palpal embolus short, triangular (Fig. 22) . . 4

3. Abdominal dorsum with 5 transverse bars (Hickman 1932: fig. 5) *H. mollipes* Hickman
– Abdominal dorsum with 5 pale, inverted, v-shaped chevrons (Fig. 5) . . . . . *H. nimorakiotakisi* sp. nov.

4. Carapace yellow brown with dark purple reticulate pattern (Fig. 1); palpal bulb larger, wider than length of cymbium and tibia combined (Figs 21–23) . . . *H. ibisca* Baehr & Smith
– Carapace yellow brown without dark purple reticulate pattern; palpal bulb smaller, as wide as or less than length of cymbium and tibia combined (Baehr & Smith 2008: figs 47–52, 56–61) 5

5. Palpal bulb shorter than length of cymbium and tibia combined, embolus triangular (Baehr & Smith 2008: figs 50–52, 59–61) ..... *H. jojo* Baehr & Smith
– Palpal bulb as wide as length of cymbium and tibia combined, embolus scooped with rounded tip (Baehr & Smith 2008: figs 47–49, 56–58, 65–67) ... *H. linnaei* Baehr & Smith

6. Abdomen with five transverse bars (Hickman 1932: fig. 5) ..... *H. mollipes* Hickman
– Abdomen with four or less inverted, v-shaped chevrons (Baehr & Smith 2008: figs 2, 4)... 7

7. Carapace with dark purple reticulate pattern; epigastric fold with posteriorly directed, u-shaped projection, posterior margin with rectangular sclerite; internal female genitalia with large posterior receptaculum divided into three circular compartments (Baehr & Smith 2008: figs 69, 70, 73, 74) ..... *H. ibisca* Baehr & Smith
– Carapace without dark purple reticulate pattern (Fig. 2); epigastric fold widely oval, posterior margin straight; internal female genitalia with elongated posterior receptaculum divided into three more triangular compartments (tapering posteriorly) (Baehr & Smith 2008: figs 68, 71, 72) ..... *H. linnaei* Baehr & Smith

Hickmanolobus ibisca Baehr & Smith, 2008 (Figs 1–4, 21–23, 34)

Hickmanolobus ibisca Baehr & Smith, 2008: 333.

Material. ♂ holotype, ♀ allotype, Queensland, Lamington NP, IBISCA site 700B, 775 m, 28.192°S, 153.124°E, 2–6 October 2006, rainforest, B. Baehr, K. Staunton, pitfall trap (♂: QM S81126, PBI_OON_6345; ♀: PBI_OON 22897, QM S55526). **Other Material:** QUEENSLAND, 1♂, IBISCA site 700C, 748 m, 28.193°S, 153.128°E, 11–20 October 2006, K. Staunton, pitfall (QM S81069, PBI_OON 6344); 1♂, IBISCA site 700D, 748 m, 28.204°S, 153.129°E, (QM S81119, PBI_OON 22718). NEW SOUTH WALES, 1♂, Cherry Tree North State Forest, 400 m, 28°54'S, 152°45'E, rainforest, April–May 1976, M. Gray, C. Horseman, pitfall trap (AM KS10314, PBI_OON 20230).

Description. See Baehr & Smith (2008).

Distribution and habitat. Rainforests in south-eastern Queensland and north-eastern New South Wales (Baehr & Smith 2008: fig. 75, Fig. 34).

Hickmanolobus nimorakiotakisi sp. nov. (Figs 5–8, 24–26, 34)

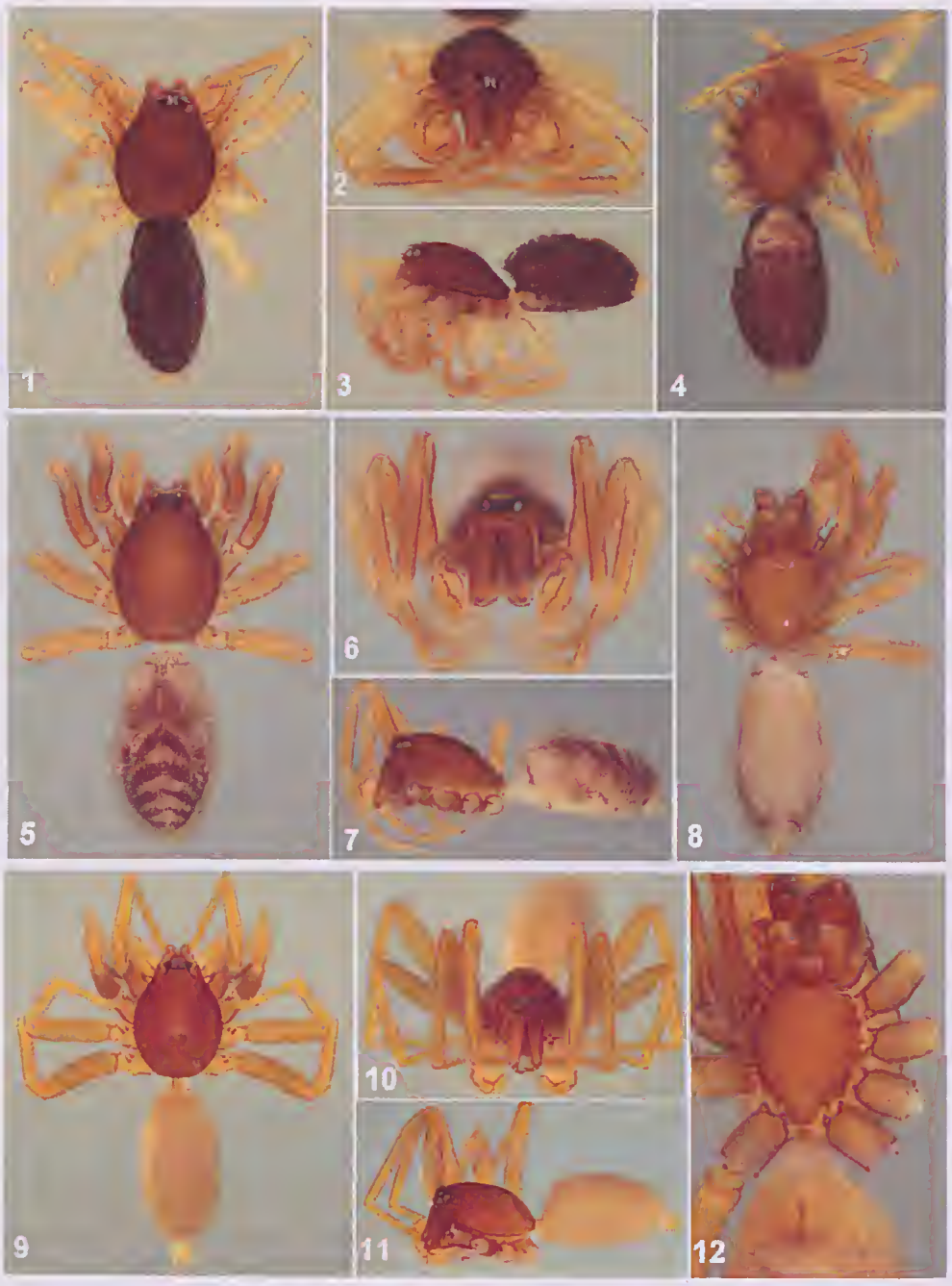
Etymology. A patronym in honour of Dr. Bill Nimorakiotakis, the Deputy Director of the Australian Venom Research Unit at the University of Melbourne, who supports spider taxonomy with great passion.

Material. Holotype ♂: Queensland, Lamington NP, IBISCA site 1100C, 28.260°S, 153.167°E, 1106m, 26 Oct 2006, C. Burwell, pyrethrum knockdown (PBI_OON 23258, QM S86313). **Other Material:** Queensland, 1♂, Mount Asplenium, 28°09'S, 152°26'E, 1290 m, 20 Jan 1993, G. Monteith, pyrethrum knockdown (PBI_OON 23261, QM S49514).

Diagnosis. This species resembles *H. mollipes* but differs in that the abdominal pattern consists of five inverted, v-shaped chevrons (Fig. 5) and the male bulb is more slender.

Description. *Male* (holotype QM S86313) (Figs 5–8). Total length 1.63. Carapace 0.76 long, 0.58 wide; abdomen 0.87 long, 0.51 wide. Carapace yellow-brown, ovoid in dorsal view, pars cephalica flat in lateral view, anteriorly narrowed to 0.5–0.75 times its maximum width, with rounded posterolateral corners, surface granulate, fovea absent, rebordered. Clypeus straight in front view, vertical in lateral view, high; ALE separated from edge of carapace by their radius. Chilum absent. Eyes six, well developed, all subequal, ALE oval, PME oval, PLE circular; posterior eye row recurved from both above and front; ALE separated by more than their diameter, ALE–PLE touching, PME touching throughout most of their length, PLE–PME separated by more than PME diameter. Endites more than three times as long as wide. Abdomen purple, with five inverted, v-shaped pale median chevrons. Legs yellow-brown. Palp (Figs 24–26), bulb pyriform with long thin embolus.

Female. Unknown.



FIGS 1–12. Orsolobidae of Lamington National Park. Habitus, 1, 5, 9, dorsal; 3, 7, 11, lateral; 2, 6, 10, frontal; 4, 8, 12, ventral. 1–4, *Hickmanolobus ibisca* Baehr & Smith; 5–8, *Hickmanolobus nimorakiotakisi* sp. nov.; 9–12, *Tasmanoonops parvus* Forster & Platnick, (9–11, male; 12, female).

Distribution. Known only from Lamington NP, south-east Queensland (Fig. 34).

Genus *Tasmanoonops* Hickman, 1930

Tasmanoonops Hickman, 1930: 97.

Type species. *Tasmanoonops alipes* Hickman, 1930 by original designation.

Diagnosis and description. See Forster & Platnick, 1985.

Tasmanoonops complexus Forster & Platnick, 1985

Tasmanoonops complexus Forster & Platnick, 1985: 71, figs 236–243, 245–248, 833, 834.

Diagnosis. From Forster & Platnick, 1985. Unlike all other species, males lack a lateral flange on the claws; females have a sclerotic plate anterior and posterior to the epigastric plate.

New material. QUEENSLAND, 1♀, Lamington NP, IBISCA site 1100D, 1140 m, 28.262°S, 153.170°E, 16–26 Jan 2007, G. Monteith, flight intercept (QM S76294).

Distribution. Known only from Lamington NP, south-east Queensland (Fig. 34).

Tasmanoonops parvus Forster & Platnick, 1985
(Figs 9–12, 27–30, 34)

Tasmanoonops parvus Forster & Platnick 1985: 60, figs 188–190, 213.

New material. QUEENSLAND, Lamington NP, 1♂, 0.6 km N Joalah Lookout, 28.367°S 153.333°E, 955 m, 21 Mar 2008, S. Wright, A. Nakamura, berlese (PBI_OON 23311, QM S86367). IBISCA site 900A, 904 m, 28.234°S 153.141°E: 1♀, 12–21 Feb 2007, K. Staunton, pitfall (PBI_OON 23318 QM S76188); 1♂, 11–20 Mar 2007, D. Putland, K. Staunton, pitfall (PBI_OON 23305 QM S86373). IBISCA site 900C, 28.240°S 153.149°E, 910 m: 1♀, 12–21 Feb 2007, K. Staunton, pitfall (PBI_OON 23314, QM S76195); 1♂, 11–20 Mar 2007, D. Putland, K. Staunton, pitfall (PBI_OON 23306, QM S86372); 1♀, 24 Jan 2008, S. Wright, berlese (PBI_OON 23309, QM S86371). IBISCA site 900D, 28.227°S 153.131°E, 920 m:1♂, 11–20 Mar 2007, D. Putland, K. Staunton, pitfall (PBI_OON 23257; QM S86383 drawing and images); 1♂, 5–8 Oct 2006, K. Staunton, B. Baehr, pitfall (PBI_OON 22549, QM S81144); 4♂♂, 11–20 Mar 2007, D. Putland, K. Staunton, pitfall (PBI_OON 23307, QM S86370; PBI_OON 23312, QM S86384). IBISCA site 1100A, 1141 m, 28.258°S 153.159°E: 1♀, 12–21 Feb 2007, K. Staunton, pitfall (PBI_OON 23317, QM S76216). IBISCA site 1100B, 1142 m, 28.259°S 153.162°E: 1♂, 2♀♀, 12–21 Feb 2007, K. Staunton, pitfall (PBI_OON 23335, QM S83626). IBSICA site 1100C, 1106 m, 28.260°S 153.167°E: 1♀, 7–11 Oct 2006, K. Staunton, pitfall (PBI_OON 23332, QM S81131); 1♀, 16–21 Jan 2007, G. Monteith, pitfall (PBI_OON 23316, QM S86118). IBISCA site 1100D, 1140 m, 28.262°S 153.170°E: 1♀, 12–21 Feb 2007, K. Staunton, pitfall (PBI_OON 23319, QM S76207); 2♀♀, 4♂♂, 11–20 Mar 2007, D. Putland, K. Staunton, pitfall (PBI_OON 23260, QM S86369, PBI_OON 23310, QM S86368); 1♀, 23 Mar–2 Apr 2007, R. Menendez, G. Monteith, malaise trap (PBI_OON 23315, QM S86119); 1♀, 27 Jan 2008, S. Wright, A. Nakamura, berlese (PBI_OON 23259, QM S86374). 1♂, 1.0 km S Binna Burra Lodge, 850 m, 28.333°S 153.3167°E, 18 Mar 2008, C. Burwell, S. Wright, K. Staunton, pitfall berlese (PBI_OON 23308, QM S86376).

Diagnosis. This species was originally described only from four females from Lamington NP (Forster & Platnick 1985). The males of this species are newly described below and can be distinguished from all other *Tasmanoonops* species by the combination of the pyriform bulb which has a long straight spiniform embolus, three dark spine-like projections and a semicircular membranous conductor, as well as by the distinctive tarsal organ.

Description. *Male* (QM S86367) (Figs 9-11). Total length 2.95. Carapace 1.35 long, 1.00 wide, abdomen 1.60 long, 0.92 wide. Carapace yellow-brown, without pattern, ovoid in dorsal view, pars cephalica flat in lateral view, anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, surface finely reticulate, rebordered. Clypeus curved downwards in front view, vertical in lateral view, low, ALE separated from edge of carapace by less than their radius. Chilum absent. Eyes six, well developed, all subequal, oval; posterior eye row recurved from both above and front; ALE separated by more than their diameter, ALE–PLE separated by less than ALE radius, PME touching throughout most of their length, PLE–PME separated by PME radius to PME diameter. Sternum longer than wide, yellow-brown, uniform, not fused to carapace, surface finely reticulate, extensions of pre-coxal triangles

FIGS 13–20. Orsolobidae of Lamington National Park. 13, habitus dorsal; 14, 17, chelicerae; 15, 18, sternae; 16, 20, tarsal claw. 13–16, *Tasmanoonops rogerkitchingi* sp. nov. male; 17–20, *Tasmanoonops complexus* Forster & Platnick, female.

present, lateral margins with narrow extensions between coxae; setae abundant, dark, needle-like, evenly scattered, originating from surface. Mouthparts: Chelicerae, endites and labium yellow-brown. Chelicerae straight, anterior face unmodified; with one tooth on both promargin and retromargin; setae dark, needle-like, evenly scattered; paturon inner margin with pairs of enlarged setae, distal region abruptly narrowed. Labium rectangular, not fused to sternum, anterior margin indented at middle. Endites twice as long as wide, distally not excavated, serrula a single row. Abdomen: ovoid, pale orange. Booklung covers large, ovoid. Pedicel tube short, unmodified, setae uniform, dark, needle-like. Legs pale orange. Palpal bulb pyriform, with long straight spiniform embolus, three dark spine-like projections and a semi-circular membranous conductor (Figs 27–30).

Distribution. Known only from Lamington NP, south-east Queensland.

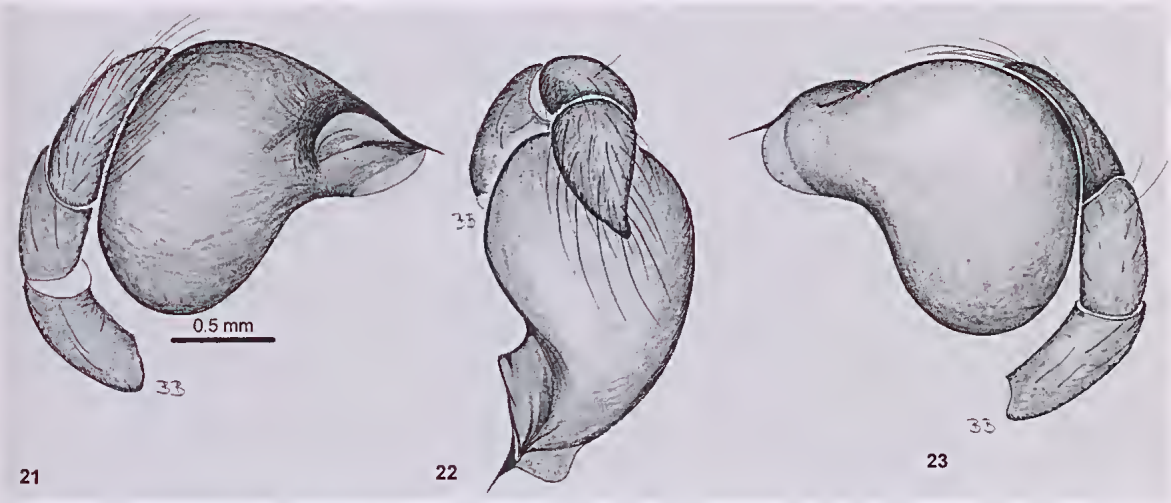
Tasmanoonops rogerkitchingi sp. nov.
(Figs 13–16, 31–33, 34)

Etymology. A patronym in honour of Professor Roger Kitching, Griffith University, who founded the IBISCA-Queensland Project.

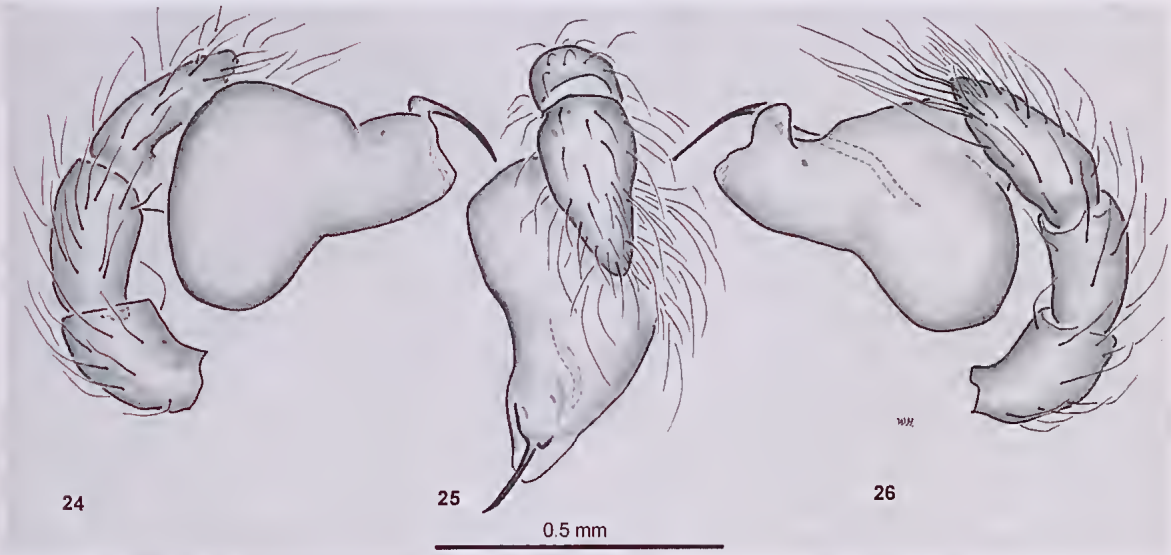
Diagnosis. The male resembles that of *T. complexus* in the general shape of the palpal bulb, but differs in the bulb having a thin semicircular embolus, a big beak-shaped process and a semicircular, membranous, cup-shaped projection.

Material. Holotype ♂: Queensland, Lamington NP, O'Reilly's, 28.233°S 153.133°E, 960 m, 16 Nov 1977, V. Davies, E. Dahms, pitfall (PBI_OON 23333, QM S86418). **Other Material:** Queensland, 1 ♂, same data as holotype (PBI_OON 23334, QM S86419).

Description. *Male* (PBI_OON 23333) (Fig. 13). Total length 4.16. Carapace 1.95 long, 1.50 wide, abdomen 2.21 long, 1.32 wide. Carapace yellow, without pattern, ovoid in dorsal view, pars cephalica flat in lateral view, anteriorly narrowed to 0.49 times its maximum width or less, with

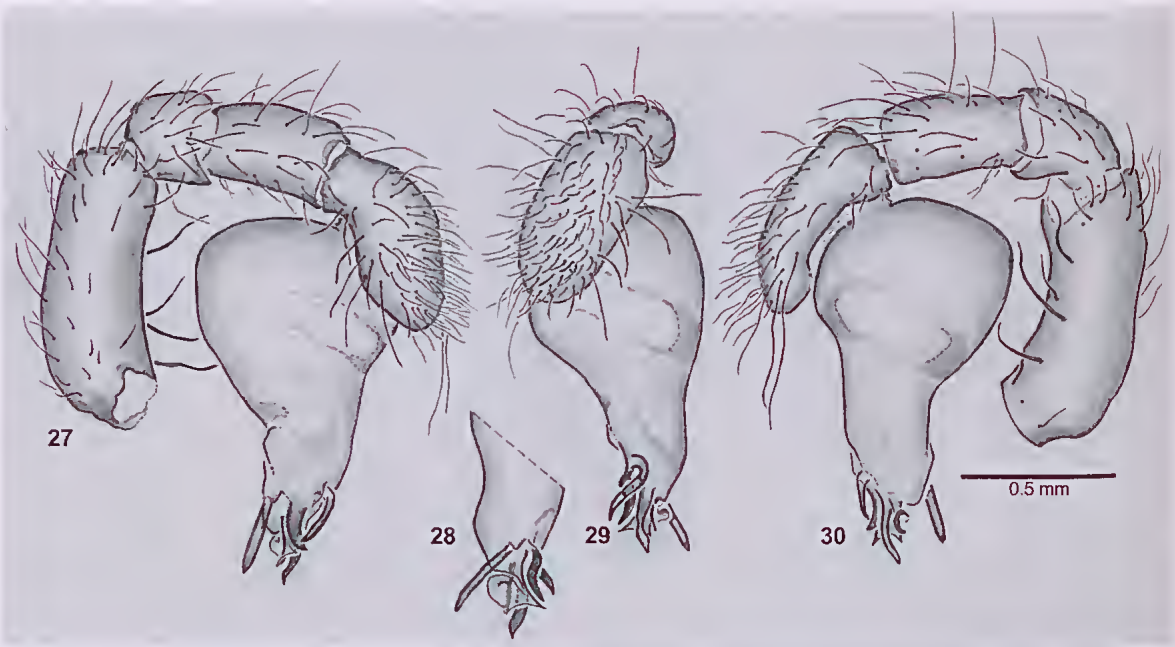


FIGS 21–23. *Hickmanolobus ibisca* Baehr & Smith. Left palp, 21, prolateral; 22, dorsal; 23, retrolateral.



FIGS 24–26. *Hickmanolobus nimorakiotakisi* sp. nov. Left palp, 24, prolateral; 25, dorsal; 26, retrolateral.

rounded posterolateral corners, surface smooth, fovea absent, lateral margin rebordered. Clypeus straight in front view, vertical in lateral view, low; ALE separated from edge of carapace by less than their radius. Chilum absent. Eyes six, well developed, all sub-equal, all eyes oval; posterior eye row recurved from both above and in front; ALE separated by more than their diameter, ALE–PLE touching, PME touching throughout most of their length, PLE–PME separated by PME radius to PME diameter. Sternum as long as wide, yellow, not fused to carapace, surface smooth, extensions of pre-coxal triangles present, lateral margins with narrow extensions between coxae



FIGS 27–30. *Tasmanoonops parvus* Forster & Platnick. Left palp, 27, prolateral; 28, ventral; 29, dorsal; 30, retrolateral.

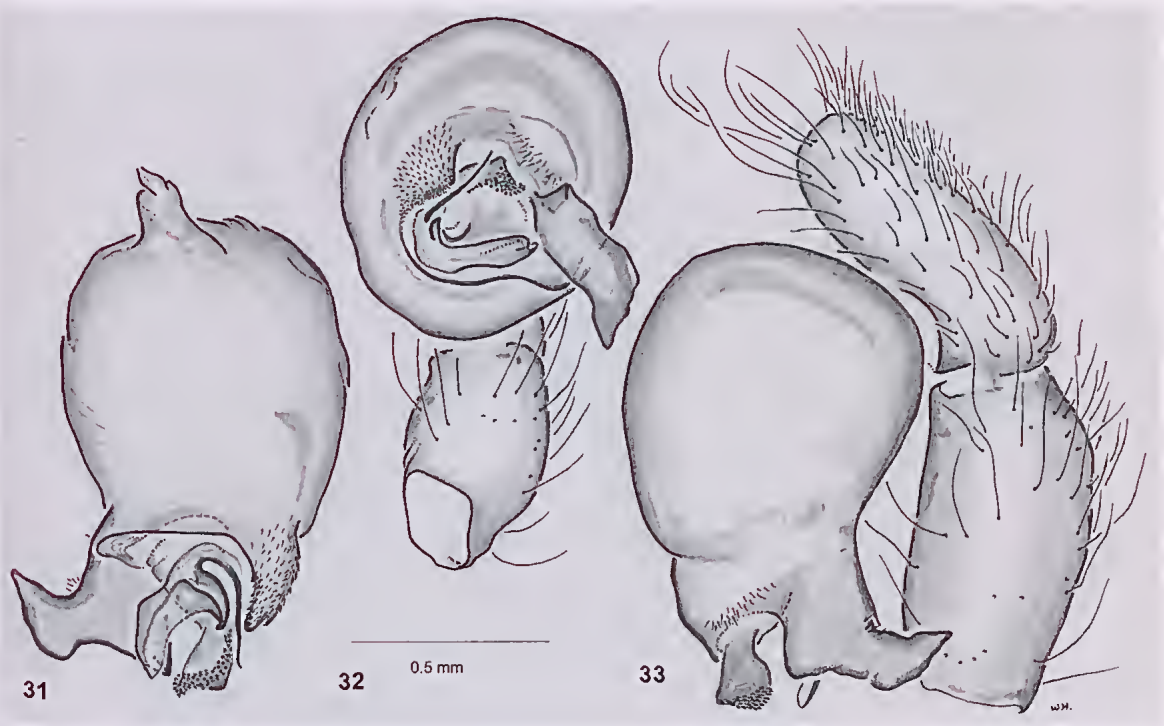
(Fig. 15); setae sparse, light, needle-like, evenly scattered, originating from surface. Chelicerae, endites and labium yellow-brown. Chelicerae straight; promargin without teeth, retromargin with two teeth (Fig. 14); setae light, needle-like, evenly scattered; paturon inner margin with pairs of enlarged setae. Labium rectangular, not fused to sternum, anterior margin indented at middle, same as sternum in sclerotisation. Endites distally not excavated, twice as long as wide, serrula a single row. Abdomen pale, ovoid; book lung covers large, ovoid; pedicel tube short, unmodified, setae uniform, light, needle-like. Colulus represented only by setae. Legs long, pale yellow, tarsal claws as in Fig. 16. Palp (Figs 31–33): Distal part of bulb with thin semicircular embolus, with big beak-shaped process and semicircular membranous cup-shaped projection.

Distribution. Known only from Lamington NP, south-east Queensland (Fig. 34).

DISCUSSION

The specimens examined in this study were mainly collected on the visionary IBISCA-Queensland Project, initiated by Prof. Roger Kitching. This project aimed to document the distributions of insects and spiders along an altitudinal gradient from approximately 300 to 1100 m above sea level, within continuous rainforest at Lamington National Park, Queensland, using rigorous ecological protocols (Kitching *et al.* 2011). During the project, intensive surveys were undertaken at four plots (A, B, C and D) within each of five altitudinal zones at approximately 300, 500, 700, 900 and 1100 m a.s.l. (see Kitching *et al.* 2011 for details).

All orsolobid specimens at Lamington were collected at higher altitudes, from between around 750 and 1150 metres above sea level: *H. ibisca* was taken in pitfall traps at three of



FIGS 31–33. *Tasmanoonops rogerkitchingi* sp. nov. Left palp, 31, prolateral; 32, ventral; 33, retrolateral.

the four plots at the 700 m a.s.l. zone; *T. parvus* at all plots at the 900 and 1100 m a.s.l. zones, except 900 B; and *T. rogerkitchingi* sp. nov. was taken only at 960 m in pitfall traps (prior to the IBISCA-Qld Project Fig. 34). The highest orsolobid diversity was found within the 1100 m a.s.l. zone with 3 species: *H. uiuorakiotakisi* collected on bark using pyrethyrum knockdowns; *T. complexus* collected with a flight intercept trap; and *T. parvus* Forster & Platnick, collected in leaf litter extracts or pitfall traps. Despite similar intensive surveys at lower altitude rainforests in Queensland's south-east corner, orsolobids remain known only from rainforest-clad mountains that reach higher than 700 m a.s.l. However, *H. ibisca* has been collected from as low as 400 m a.s.l. from a site in rainforest in northern New South Wales about 80 km south and 60 km west of the IBISCA-Qld sites. Apart from being more southerly, the aspect of this site may well have been southerly and hence cooler, explaining the occurrence of *H. ibisca* at this relatively low elevation. Earlier studies at Lamington National Park (e.g., Davies 1977), although thorough and intensive, were not so rigorously conducted as IBISCA-Qld and were conducted only at higher elevations (900 m a.s.l. and higher) and hence data from them are useful only as qualitative measures of diversity. Davies (1977) reported only one species of *Tasmanoonops* (here described as *T. rogerkitchingi* sp. nov.) from 960 metres elevation.

Consequently, it would appear that orsolobid spiders of Lamington National Park are effectively mid to high elevation specialists and may be useful candidates for incorporation in programs designed to help monitor the effects of climate change, especially those of global warming. We suggest that the distribution of

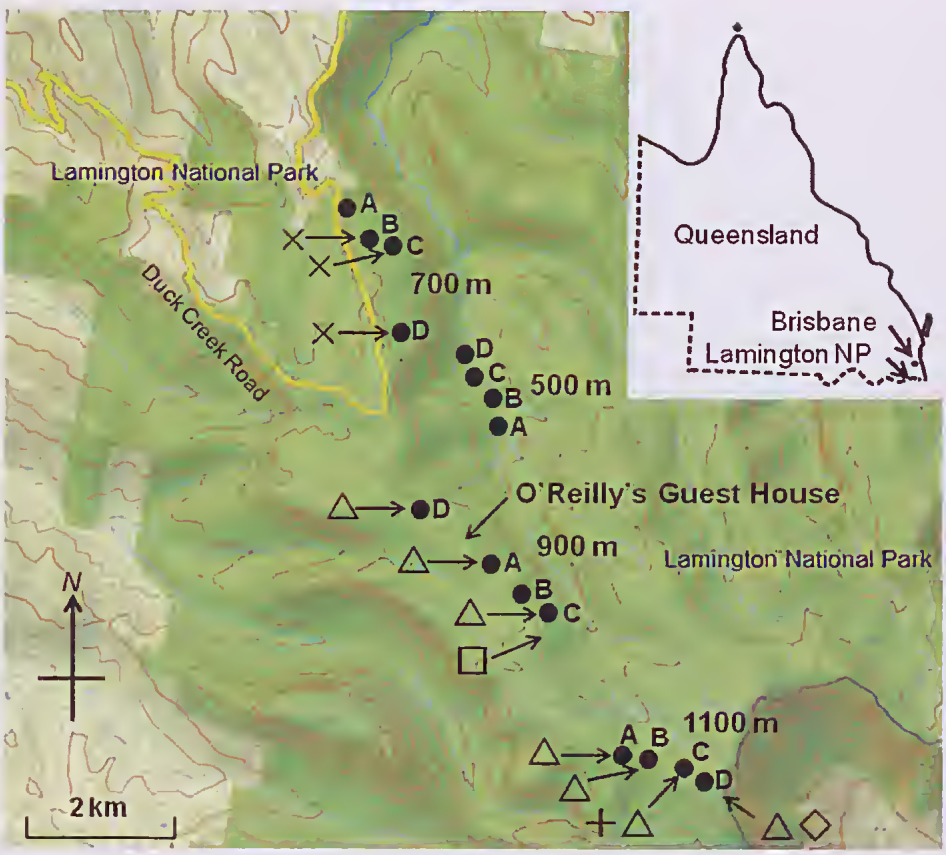


FIG. 34. Known distribution of five species of Orsolobidae within Lamington National Park. ×, *Hickmanolobus ibisca*; +, *H. nimorakiotakisi*; ◇, *Tasmanoonops complexus*; △, *T. parvus*; □, *T. rogerkitchingi*. Solid circles indicate the locations of IBISCA-Queensland Project study plots which are labelled A-D within their altitudinal zones; 500, 700, 900 and 1100 m a.s.l. (see also Fig. 1 in Kitching *et al.* 2011 for IBISCA-Qld plot locations). Note *T. rogerkitchingi* was not collected from an IBISCA-Qld plot.

orsolobid species along the IBISCA-Qld gradient is restricted by the higher temperatures and lower humidities at lower altitudes. As the climate warms, orsolobid species are predicted to shift to higher elevations in order to track their preferred temperatures and humidities. These predicted changes can be monitored through consistent standardised sampling. The Orsolobidae are an ideal target group for monitoring the impacts of climate change at Lamington NP. In addition, the species apparently restricted to the highest elevations along the gradient may be under threat of at least local extinction in the relatively near future.

ACKNOWLEDGEMENTS

Most of the specimens examined in this study were collected during the IBISCA-Queensland Project and as such we are grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University,

the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We would like to thank the IBISCA-Queensland team, especially, Queensland Museum staff, C. Burwell, A. Nakamura, G. Monteith, S. Wright, as well as D. Putland and K. Staunton, for their excellent collecting work, and A. Nakamura and C. Burwell for producing the distribution map. This paper is dedicated to people and institutions that support taxonomic science with their encouragement. This paper would not have been completed, without the support of IBISCA-Queensland and the National Science Foundation's PBI (Planetary Biodiversity Inventory) program provided through grant DEB-0613754.

LITERATURE CITED

Baehr, B.C. & Smith, H.M. 2008. Three new species of the Australian orsolobid spider genus *Hickmanolobus* (Araneae: Orsolobidae). *Records of the Western Australian Museum* **24**: 325–336.

Cooke, J.A.L. 1965. Spider genus *Dysdera* (Araneae: Dysderidae). *Nature*: **205**: 1027–1028.

Davies, V.E. 1977. Spiders. *In*, Covacevich, J. (Ed.), *Fauna of Eastern Australian Rainforests II. Preliminary report on sites surveyed by the Queensland Museum in southeastern and far northeastern Queensland, with additional results from sites surveyed previously in northeastern Queensland.* (Queensland Museum: Brisbane).

Forster, R.R. & Forster, L.M. 1999. *Spiders of New Zealand and their Worldwide Kin*. (University of Otago Press: Dunedin).

Forster, R.R. & Platnick, N.I. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. *Bulletin of the American Museum of Natural History* **181**: 1–229.

Griswold, C.E. & Platnick, N.I. 1987. On the first African spiders of the family Orsolobidae (Araneae, Dysderoidea). *American Museum Novitates* **2892**: 1–14.

Hickman, V.V. 1930. Studies in Tasmanian spiders. Part IV. *Papers and Proceedings of the Royal Society of Tasmania* **1929**: 87–122.

1932. Studies in Tasmanian Spiders. Part V. *Papers and Proceedings of the Royal Society of Tasmania* **1931**: 20–31.

1979. Some Tasmanian spiders of the families Oonopidae, Anapidae and Mysmenidae. *Papers and Proceedings of the Royal Society of Tasmania* **113**: 53–79.

Kitching, R.L., Putland, D.A., Ashton, L.A., Laidlaw, M.J., Boulter S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.

Platnick, N.I. 2011. The World Spider Catalog, Version 11.5. American Museum of Natural History, New York. http://research.amnh.org/entomology/spiders/catalog/index.html.

Platnick, N.I. & Brescovit, A.D. 1994. A new genus of the spider family Orsolobidae (Araneae, Dysderoidea) from Brazil. *American Museum Novitates* **3112**: 1–6.

Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient

Darren BITO

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: dbito@binatang.org.pg

Vojtech NOVOTNY

Czech Academy of Sciences and University of South Bohemia, Ceske Budejovice, Czech Republic.

Chris J. BURWELL

Akihiro NAKAMURA

Biodiversity Program, Queensland Museum, PO Box 3300, South Brisbane Qld 4101; Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia.

Roger L. KITCHING

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia.

Frode ØDEGAARD

Norwegian Institute for Nature Research Trondheim, Norway.

Citation: Bito, D., Novotny, V., Burwell, C.J., Nakamura, A., Kitching, R.L. & Ødegaard, F. 2011 20 19: Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient. *Memoirs of the Queensland Museum – Nature* 55(2) 451-461. Brisbane. ISSN 0079-8835.

ABSTRACT

Climate change is predicted to not only cause shifts in the latitudinal and altitudinal distribution of species, but also changes in trophic interactions. Studying changes in herbivory and herbivore and predator pressure along altitudinal gradients may assist our understanding of the complex trophic interactions and their responses to future climate change. As part of the IBISCA-Queensland Project, we tested the hypothesis that ant predation pressure influences the abundance of herbivores which in turn influences herbivory in the understorey of subtropical rainforest and that these relationships are modified by altitude. We used the occupancy of ants at tuna baits as a measure of predation pressure, herbivorous beetles as representatives of herbivores, and the extent of damage to mature leaves as a measure of herbivory. Ant predation pressure was the greatest at 300 m above sea level and declined with increasing altitude but only at ground level. In contrast, ant predation pressure on understorey foliage was not related to altitude and was always much lower than that on the ground. Neither altitude nor ant predation pressure at ground or understorey levels significantly influenced the abundance of herbivorous beetles. However, the species richness of herbivorous beetles significantly decreased with increasing altitude, and ground-level ant predation pressure negatively related to beetle species richness, after controlling for the effect of altitude. Levels of herbivory were not related to beetle abundance, whereas it was significantly negatively related to beetle species richness. This was however, opposite to our prediction that increased beetle species richness would increase leaf herbivory. Consequently, we found little evidence for the cascading effects of ants on herbivory in our study system. We suggest that future studies examine other groups of foliage-feeding insects such as lepidopteran larvae and Orthoptera, and the importance of other natural enemies, including parasitoids as well as non-specific predators. ❐ *elevation, Formicidae, Coleoptera, herbivory, predation.*

Arboreal insect assemblages within tropical ecosystems are dominated by ants in terms of both biomass and the number of individuals (Stork 1988; Hölldobler & Wilson 1990). Often the entire forest canopy fauna is dominated by large ant colonies (Stork 1991; Davidson 1997) many of which play a significant role in plant defenses by attacking invertebrate and mammalian herbivores and by interrupting encroaching vegetation (Huxley 1982). Although the role of ants as specialised predators is limited to some subfamilies and genera (Tobin 1991; Davidson 1997; Blüthgen *et al.* 2000; Dejean *et al.* 2000), a number of studies have demonstrated that ants represent important generalist predators of insect herbivores. For example, ants in lowland forests of New Guinea were responsible for 77% of the total predation of baits of live termites set on the foliage of *Ficus* plants (Novotny *et al.* 1999), while Floren *et al.* (2002), using caterpillars as baits in tropical lowland rain forest in Sabah, Malaysia, found that, on average, 85% of ant individuals in the canopy of trees were predacious. Further, using insecticidal fogging and direct observations, the latter study suggested that arboreal ants were responsible for an observed scarcity of less mobile arthropods in the rainforest canopy. Low numbers of less mobile holometabolous arthropods, such as lepidopteran larvae, were associated with ant dominance. In contrast, highly mobile hemimetabolous nymphs occurred regularly and in large numbers on ant dominated trees (Floren *et al.* 2002).

Ant assemblages in tropical forests have markedly reduced species richness and abundance at higher elevations (Brown 1973; Fisher 1996; Bruhl *et al.* 1999). This upward depauperisation of ant assemblages along altitudinal gradients is anticipated to be associated with a decrease in predation pressure on herbivorous insects. It is of interest and significance, therefore, to investigate the rates of herbivory across an altitudinal gradient in relation to predation pressure due to ants.

Environmental gradients across latitude and altitude, in Australia and elsewhere, are increasingly being used as surrogate systems for predicting changes in arthropod assemblages in response to changing climatic conditions (Gutiérrez & Menéndez 1998; Bale *et al.* 2002; Andrew & Hughes 2004, 2005). In Australia, a rise in continental average temperature of ~0.8°C has already occurred since 1910 (Nicholls 2006). Our emerging understanding is that as temperatures rise, species are likely to shift their distributions from lower to higher altitudes, and polewards from lower to higher latitudes (Thomas *et al.* 2006). The consequences of such responses will have drastic impacts on existing biodiversity and the ecosystem services they provide (Walther *et al.* 2002).

This study investigated whether the extent of herbivory in understorey vegetation is related to the abundance and richness of insect herbivores, and whether these herbivores are in turn influenced by top-down impacts of predator pressure exerted by ants. We also tested whether these relationships are mediated by differences in altitude. Here we present preliminary results using herbivorous beetles as representatives of herbivores.

METHODS

Our study was carried out as part of the IBISCA-Queensland Project (Kitching *et al.* 2011) which established permanent survey plots along an altitudinal gradient at Lamington National Park, Queensland, Australia. Four replicated plots (20 m x 20 m quadrat) were established within each of five altitudinal zones, at approximately 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). Plots were located within continuous forest spanning araucarian complex notophyll vine forest (300 m a.s.l.), warm subtropical complex notophyll vine forest (500 and 700 m), cool subtropical complex notophyll vine forest (900 m) and simple microphyll fern forest (1100 m) (Laidlaw *et al.* 2011). Long-term

monthly rainfall averages range from about 50 to 250 mm with most falling in summer (December-February) and rainfall increases with increasing elevation (Strong *et al.* 2011).

Ant predation pressure. To assess predator pressure we used the response of ants to food baits. Baits consisted of fragments of tuna (canned in oil) placed in a folded piece of tissue paper (5 cm x 5 cm). Baits were secured with stainless steel entomological pins onto a leaf or twig of an understorey plant ('foliage bait') or onto leaf litter or woody debris on the ground ('ground bait') beneath the foliage bait. A total of approximately 25 pairs (of tuna baits foliage and ground) were placed at random points within each study plot and exposed for 30 minutes (as per Novotny *et al.* 1999). The number of tuna baits attacked by ants was counted and voucher specimens of each ant morphospecies were collected and stored in 70% ethanol for later identification. Sampling was conducted in the austral spring of 2006 (6–24 October). In total, 970 tuna baits were set, 483 in understorey foliage and 487 at ground level across the five altitudinal zones. For logistical reasons, tuna baits were deployed at only two of the four survey plots at 700 m (700C and D, see Kitching *et al.* 2011).

Herbivore pressure in the understorey. The abundance of herbivorous beetles was used as a surrogate for herbivore pressure on understorey plant foliage. Beetles were sampled in the spring of 2006 (6-24 October), by beating 'vegetation' using a 1.5 m long beating stick and a 1 m^2 nylon sheet for collecting the falling material (see Ødegaard & Diserud 2011). 'Vegetation' included all structures including foliage and the trunks of large trees to thin branches, both living and dead. Each sample was obtained by beating all reachable vegetation on both sides of a 20 m long transect starting just outside the 20 m by 20 m standard IBISCA plots and walking in a straight line away from the plot. A forest area of approximately 3 x 20 m (60 m^2) and a forest volume of 60 m^2 x 3 m height (180 m^3) was covered by each sample. Ten samples (transects) were taken at each plot, all performed in different directions from the same starting point to prevent re-beating of the same area. Accordingly, a total of 200 samples was obtained (10 samples x 20 plots), but the 10 samples collected at each plot were pooled before analyses. Beetles were sorted to family and morphospecies. Although beetles representing various feeding guilds were collected (see Ødegaard & Diserud 2011), only herbivorous beetles were used for the present study. Both the total abundance and species richness of herbivorous beetles were recorded for each plot.

Measurement of foliage damage. Foliage damage due to herbivory within understorey vegetation was estimated from a random selection of leaves taken during spring (6-24 October) 2006. Leaf samples were collected from all four plots at each altitude, except at 700 and 900 m a.s.l. where only two and three plots were sampled respectively. At each plot, we randomly hand collected mature leaves of understorey vascular plants. Leaves from each plot were thoroughly mixed in a large cardboard box. Leaves were then picked from the box and progressively laid out flat, with the edges of individual leaves slightly separated, on a 48 cm x 48 cm square frame with a white background. Eight frames of leaves were compiled for each plot, giving a total of 136 frames across the five altitudinal zones, with between 16 to 70 individual leaves per frame.

Frames were photographed using an 8 megapixel digital camera and images imported into Adobe Photoshop version 6 (Adobe Systems Inc. 2001). Missing sections on the edges of leaves were reconstructed, based on the shapes of intact leaves of the same species. In addition to missing sections, leaf damage also included desiccated areas caused by leaf mining and leaf skeletonising larvae, and these areas were converted to white. Images were then contrasted to produce a black (undamaged leaf areas) and white (damaged leaf areas) image. ImageJ software (Rasband 2003) was used to measure both damaged leaf area and total leaf area (i.e. damaged and undamaged leaf area

combined). The proportion of leaf damage was calculated by dividing the damaged leaf areas by the total leaf areas summed across the eight frames per plot.

Data analysis. Initially we conducted analyses using altitude as a categorical variable. We first investigated differences in predation pressure (proportion of baits attacked) and species richness (number of species attracted to baits) of ants across the five altitudinal zones, using two-way ANOVA with altitude and stratum (ground versus understorey) as fixed factors. Herbivore pressure (abundance and species richness of herbivorous beetles) and understorey leaf damage were examined by analysis of covariance (ANCOVA) to test for the presence of top-down effects of predation pressure and herbivore pressure, in conjunction with the effect of altitude. Ant predation pressure was included as a covariate in the analysis of herbivore pressure, and herbivore pressure (as species richness or abundance of herbivorous beetles) as a covariate in the analysis of leaf damage. We assumed no interaction between the main factor (altitude) and the covariates. Due to the unequal number of replicated samples (ant data missing from some 700 m plots and leaf damage missing from some 700 and 900 m plots), type III sum of squares was used to calculate *F* statistics. When we found a significant effect of altitude, *post-hoc* pair-wise comparisons were made using Tukey's HSD tests.

We also conducted multiple regression analysis with altitude as a continuous variable, using the actual altitudes of the study plots (see Kitching *et al.* 2011 for these values). Separate analyses were conducted for five different response variables; ground-level ant predation pressure, understorey-level ant predation pressure, herbivorous beetle abundance, herbivorous beetle species richness and the proportion of damaged leaf area. Analyses of ant predation pressure (ground and understorey) included only altitude as an explanatory variable. Analyses of both beetle abundance and species richness included three explanatory variables; altitude, and ground and understorey ant predation pressure. Analysis of the proportion of leaf damage also included three explanatory variables; altitude, and herbivorous beetle abundance and species richness. A stepwise selection procedure, with *P* values of 0.05 for inclusion and 0.10 for exclusion, was used to construct the model which best explained the variation in each response variable.

Abundances of herbivorous beetles were log-transformed before analyses, but neither proportional (ant predation pressure and leaf damage) nor species richness of herbivorous beetles were transformed as they were approximately normally distributed without outliers. ANOVAs and ANCOVAs were conducted using the general linear model function, and regression analyses using the linear regression function within SPSS ver. 17 (2009).

RESULTS

Ant predation pressure. Across the five altitudinal zones, 271 of 487 (56%) baits at ground level were attacked by ants, while only 32 of 483 (7%) baits on understorey foliage were attacked. While we found significant effects of both altitude and stratum (ground versus understorey) on ant species richness and predation pressure, their interaction was also highly significant (Table 1). At ground level, we found the greatest number of ant species (mean 9.5) and the greatest proportion of baits attacked (mean 93%) at 300 m a.s.l. and the lowest at 1100 m (1.0 species, 6% of baits) (Fig. 1). However, in the understorey, neither species richness nor predation pressure differed significantly among altitudinal zones, although they were both lowest at 1100 m (Fig. 1). Linear regression confirmed these patterns, with a significant decrease in the proportion of ground-level baits attacked with increasing altitude (t = -5.95, correlation coefficient = -0.84, P<0.001), and no relationship between altitude and the proportion of foliage baits attacked.

TABLE 1. Summary results of ANOVA showing *F* and *P* values of altitude, stratum (ground versus understorey) and their interaction effects on ant species richness (number of ant species attracted to baits) and predation pressure (proportion of baits occupied by ants). Degrees of freedom for altitude, stratum, interaction and error are 4, 1, 4, and 26 respectively. Significant *P* values are shown in bold.

	Altitude		Stratum (ground vs understorey)		Interaction	
Dependent variable	*F*	*P*	*F*	*P*	*F*	*P*
Ant species richness	6.4	**0.001**	37.3	**<0.001**	4.0	**0.011**
Ant predation pressure	11.6	**<0.001**	82.5	**<0.001**	9.0	**<0.001**

TABLE 2. Summary results of ANCOVA showing *F* and *P* values of effects of altitude and covariate on abundance and species richness of herbivorous beetles and understorey herbivore damage (proportion of leaf area damaged by herbivores). Degrees of freedom for altitude and covariate are 4 and 1 respectively. Degrees of freedom of error term is 12 for herbivorous beetle abundance and species richness and 11 for herbivore leaf damage. Significant *P* values are shown in bold.

	Altitude		Covariate		
Dependent variable	*F*	*P*		*F*	*P*
Herbivorous beetle abundance	0.181	0.944	Ant predation pressure (ground)	0.001	0.973
	0.433	0.782	Ant predation pressure (understorey)	1.076	0.320
Herbivorous beetle species richness	7.057	0.004	Ant predation pressure (ground)	3.882	0.072
	4.186	0.024	Ant predation pressure (understorey)	0.046	0.834
Herbivore leaf damage	1.809	0.197	Herbivorous beetle abundance	0.976	0.344
	0.707	0.604	Herbivorous beetle species richness	0.461	0.511

Herbivory pressure. Beating understorey vegetation yielded a total of 4854 beetles representing 604 species. Herbivorous beetles represented 1212 individuals (25% of total) from 132 species (22%). The mean abundance of herbivorous beetles was greater at the highest altitudes (900 and 1100 m) (Fig. 2a). However, ANCOVA analysis found no significant relationship between altitude, nor the covariates (ant predation pressure at ground or understorey level), and the abundance of herbivorous beetles (Table 2). In contrast, the species richness of herbivorous beetles was significantly related to altitude (Table 2) with fewer herbivorous beetle species at higher altitudes (Fig. 2b) in spite of their higher abundances. Neither ground nor understorey ant predation pressure were related to herbivorous beetle species richness (Table 2). Simple scatter plots between the covariates (ant predation pressure at the ground and in the understorey) and herbivorous beetle abundance and species richness showed no apparent relationships, consistent with the results of ANCOVA (Fig. 3).

Stepwise multiple linear regression selected none of the explanatory variables for herbivorous beetle abundance. In contrast, species richness of herbivorous beetles was significantly negatively associated with increasing altitude (t = -4.72, P<0.001). After controlling for the effect of altitude, beetle species richness was also negatively related to ant predation pressure on the ground (t = -3.52, P = 0.003) but not on understorey vegetation.

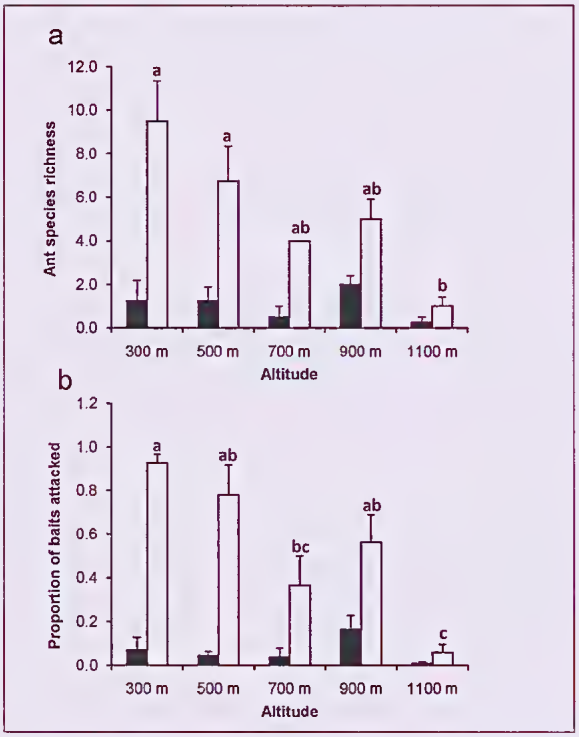


FIG. 1. Mean (+SE) proportion of tuna baits on understorey foliage (solid bars) and at ground level (open bars) attacked by ants within 30 minutes of exposure across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.). Results of post-hoc Tukey tests are shown with different letters indicating significant differences between altitudinal zones.

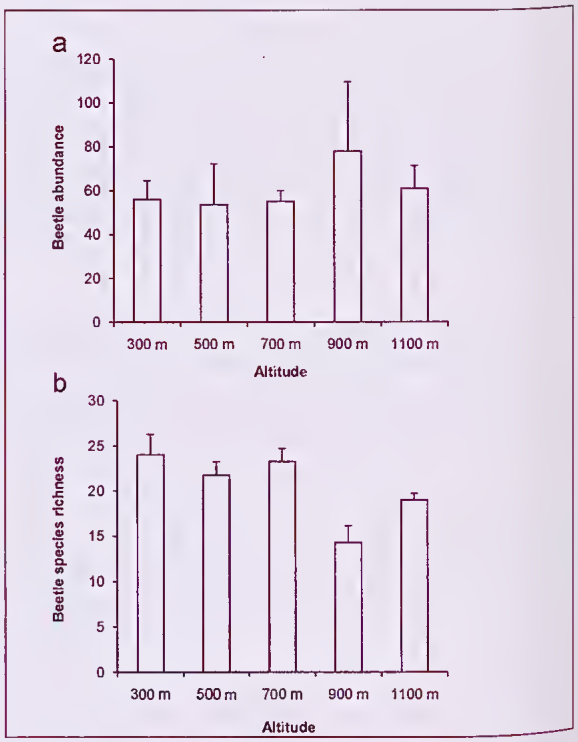


FIG. 2. Mean (+SE) abundance (a) and species richness (b) of herbivorous beetles collected from understorey vegetation across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.).

Herbivore damage of understorey leaves. A total of 5584 leaves was collected from the understorey across the five altitudes, representing 191 109 cm^2 of foliage including 9128.6 cm^2 lost to herbivory. The foliage area lost to herbivory within plots ranged between 2.54 and 9.37%. Although mean leaf damage was lowest at 300 and 700 m (Fig. 4), ANCOVA failed to detect significant altitudinal differences (Table 2). ANCOVA also failed to detect any significant effects of the covariates (abundance or species richness of herbivorous beetles) on the proportion of leaf damage (Table 2). In contrast, multiple regression found that the proportion of leaf damage was significantly negatively related to herbivorous beetle species richness (t = -2.34, P<0.034). However, this relationship was not consistent within each altitudinal zone (Fig. 5).

DISCUSSION

Ant predation pressure. In tropical forests, ant species richness and abundance are generally reduced at higher altitude (Brown 1973; Fisher 1996; Bruhl *et al.* 1999). Similarly we found a significant reduction in ant species richness and predation pressure (proportion of baits occupied by ants) with increasing altitude. However, this was apparent only for epigaeic ants, and ant species richness and predation pressure in the understorey were much lower than on the

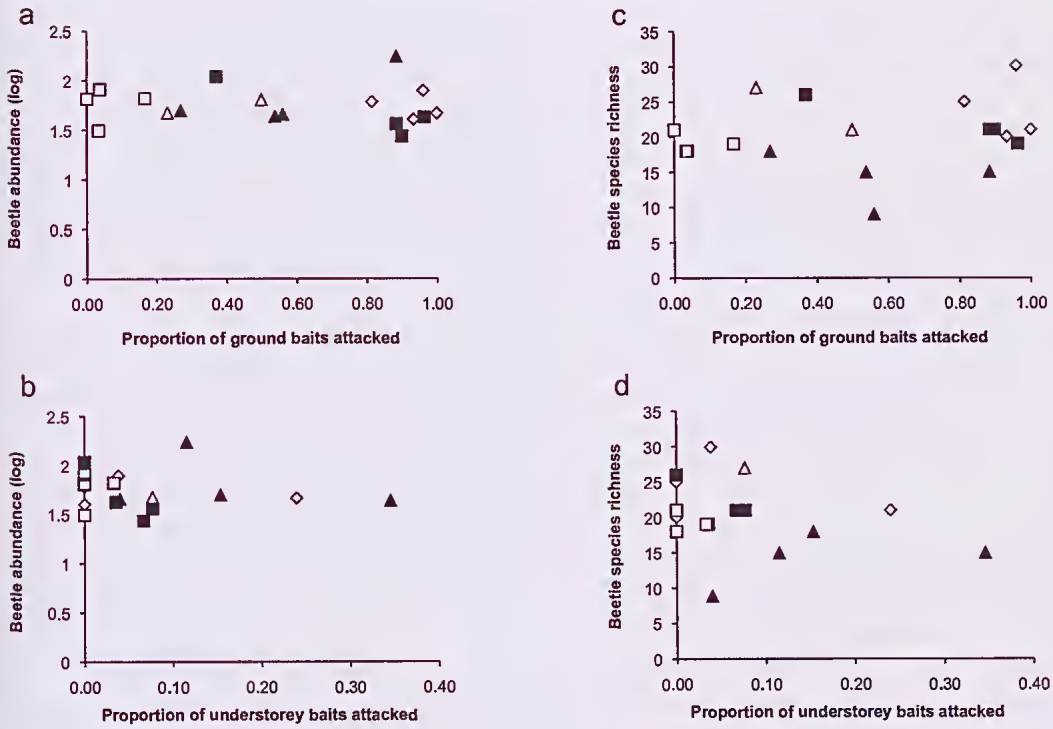


FIG. 3. Relationships between ant predation pressure (proportions of baits attacked) and herbivorous understorey beetles across altitude (◇, 300 m; ■, 500 m; △, 700 m; ▲, 900 m; and □, 1100 m a.s.l.). Beetle abundance was plotted against both proportion of baits attacked on the ground (a) and on understorey foliage (b). Similarly beetle species richness was plotted against baits attacked on the ground (c) and in the understorey (d).

ground, with no significant differences across altitudes (most plots having less than 6% of tuna baits occupied by ants). The low level of ant activity in the understorey observed in this study is in agreement with previous studies that have found low abundance and species richness of arboreal ants in Australia's subtropical rainforests (Majer 1990; Majer *et al.* 2001).

This low observed ant predation pressure in the understorey, especially at lower altitudes, contrasts with lowland tropical forests where abundances of predatory ant species on trees are usually very high. For example, in lowland rainforest in Sabah, Malaysia, ants average 60% of all arthropods of a tree community (Floren & Linsenmair 1997) and on average 85% of ant

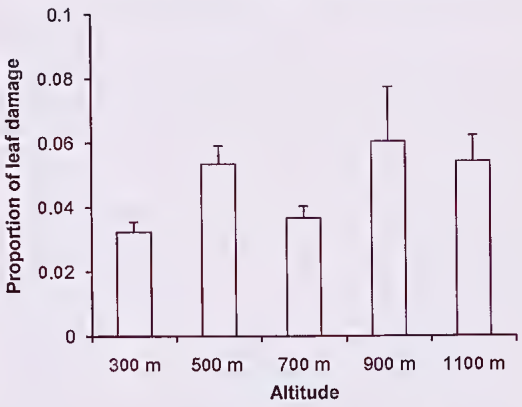


FIG. 4. Mean (+SE) herbivore damage (proportion of leaf area damaged) on understorey plant foliage across five altitudinal zones (300, 500, 700, 900 & 1100 m a.s.l.).

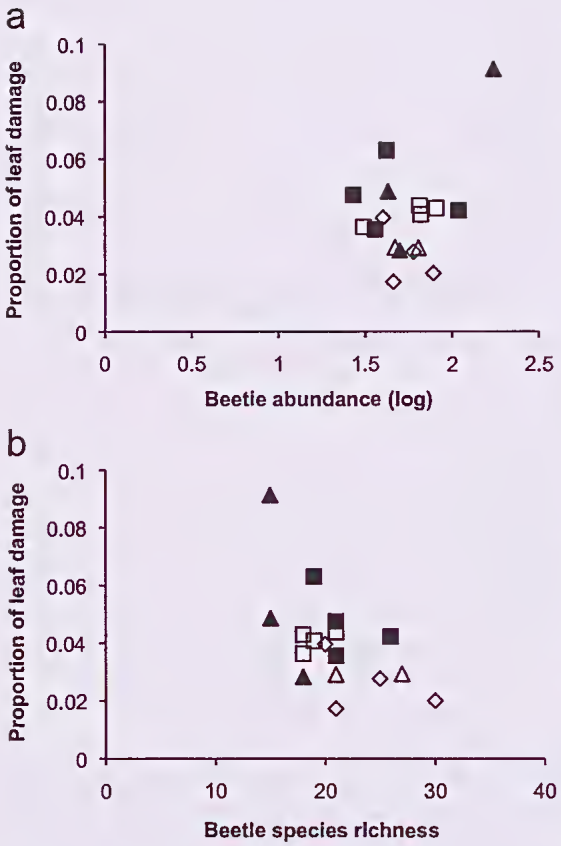


FIG. 5. Relationships between understorey leaf damage and herbivorous understorey beetles across altitude (◇, 300 m; ■, 500 m; △, 700 m; ▲, 900 m; and □, 1100 m a.s.l.). The proportion of leaf area damaged was plotted against the abundance (a) and species richness (b) of beetles.

individuals per tree are predacious (Floren *et al.* 2002). However, there can be substantially less ants in the understorey compared to the canopy, for example in rainforest in Cameroon ant density in the understorey can be ten times less than in the canopy (Basset *et al.* 1992). This reduced abundance in the understorey is reflected in reduced predation pressure as Olson (1992) recorded predation rates of 26% in the understorey compared to 75% in the canopy in primary rainforest in Cameroon. This understorey predation rate is similar to that in the understorey of rainforest in Papua New Guinea where Novotny *et al.* (1999) found that during the day, 32% of tethered termites on fig foliage were attacked by ants within 30 minutes. Even though ant predation pressure in the understorey of tropical forests is lower than in the canopy, it still appears to be much greater than predation pressure in the understorey of subtropical rainforest in our study area.

We suspect that the extremely low predation pressure observed in this study is plausible, although it could be argued that it was due to short-comings in our sampling methods. First, tuna baits were placed only within the 20 x 20 m IBISCA-Qld plots, and large colonies of ants that may be nesting within larger tree trunks or canopy foliage may not have been sampled. Second, a bait exposure time of 30 minutes may be too short for subtropical arboreal ants to discover them (although it was sufficient for ground baits to attract large number of ants). Third, the study was conducted only during daylight hours thus excluding nocturnal predatory ant species. The third issue, however, may not be relevant as similar studies in tropical forests have shown that predatory ant activity is higher during the day (e.g. Novotny *et al.* 1999). Despite these issues, we believe that our results are best explained by a lack of dominant ant species (see Majer 1990) which are typical of tropical lowland rainforest and which substantially contribute to the high abundances of ants in these ecosystems.

Herbivory pressure. Although we anticipated some effect of ant predation pressure on herbivores, we did not find strong evidence supporting this hypothesis. The only significant relationship that we found was a negative influence of ground-level ant predation pressure on beetle species richness, after controlling for the effect of altitude. Although this may suggest that some species of herbivorous beetles are susceptible to increased levels of ant activity at ground-level, overall beetle abundance was

unaffected by ground- or understorey-level ant predation pressure.

Given that we observed very low ant activity in understorey vegetation, the lack of a relationship between understorey ant predation pressure and herbivorous beetles is not all that surprising. In addition, adult herbivorous beetles that we used to represent herbivores may not be particularly sensitive to ant predation even if predation pressure had been more intense than observed. Many herbivorous beetle species have differing larval and adult feeding strategies (Reid 2006), which may reduce the extent of direct interactions with predacious ants on the ground and foliage. In addition, more mobile herbivores such as adult beetles and other winged insects such as stick insects and orthopterans, may not be particularly vulnerable to ant predation. Ant predation may have a stronger impact on the less mobile larvae of beetles or moths and butterflies.

Herbivore damage of understorey plant leaves. We found no significant effect of altitude on the extent of leaf damage. The observed pattern was rather idiosyncratic, with lower herbivore damage observed at 300 and 700 m and greater damage at 500, 900 and 1100 m a.s.l. The extent of leaf damage across the altitudinal zones did not coincide with observed patterns of abundance and species richness of herbivorous beetles. We found fewer beetle species at higher altitudes, but greater herbivory was observed there. Similarly, multiple regression detected a significant negative relationship between the species richness of herbivorous beetles and the proportion of leaf damage. We initially anticipated that increased herbivore pressure would result in greater levels of leaf damage, but the observed pattern was opposite to our expectation. The basis for the observed inverse relationship between beetle richness and levels of herbivory is unclear, but our results should be interpreted carefully as adult beetles are not the only insects causing leaf damage. In addition, most beetle species with foliage feeding adults belong to the subfamily Chrysomelinae (Chrysomelidae) and the broad-nosed weevils (Curculionidae), and these beetles were rare and species poor within our study sites at Lamington National Park (Ødegaard, personal observations).

Our results also require careful interpretation due to the way we measured leaf damage. Our leaf sampling involved the random collection of damaged and undamaged leaves still attached to plants. Consequently our measure of leaf damage did not account for leaves that were fully consumed or abscissed due to herbivory, potentially causing underestimation of herbivory. Ideally herbivore damage should be measured over the entire life span of each leaf (e.g. Lowman 1987). In addition, measuring leaf damage is complicated by leaf longevity. As leaves age they generally become less palatable to herbivores and most damage is sustained within a short period of time when the leaf is young (Coley 1980, Lowman 1985). This complicates trying to relate leaf damage of mature leaves with herbivore pressure. As leaf longevity increases there is more potential for a temporal mismatch between herbivore pressure at the time of sampling and herbivore pressure experienced when leaves were damaged.

We initially hypothesised that ant predation pressure would influence the herbivore pressure which in turn would influence the extent of leaf damage in the rainforest understorey and that these relationships would be modified by altitude. Specifically arboreal ant abundance was expected to decline with increasing altitude, ultimately resulting in an increase in herbivory with increasing altitude. However, we found very little evidence for the cascading effects of ants on herbivory in our study system, the subtropical rainforest of south-eastern Queensland. This may largely result from the depauperate arboreal ant fauna of these forests, across all altitudes. Predatory arboreal ants are much more abundant in tropical forests, where a similar study may shed more light on the role of altitude in modifying the influence of ants on herbivore dynamics. Our study begs the question of what drives herbivore

dynamics in subtropical rainforest. We suggest that future studies examine other groups of foliage-feeding insects such as lepidopteran larvae and Orthoptera, and the importance of other natural enemies of herbivores, including parasitoids as well as other non-specific predators.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. This work would not have been possible without the assistance of numerous volunteers and we thank all IBISCA-Queensland participants for their collaboration.

LITERATURE CITED

Adobe Systems Inc. 2001. *Adobe Photoshop version 6.0.1.* (Adobe Systems Incorporated: San Jose).

Andrew, N.R. & Hughes, L. 2004. Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change. *Ecological Entomology* **29**: 527-542.

2005. Arthropod community structure along a latitudinal gradient: implications for future impacts of climate change. *Austral Ecology* **30**: 281-297.

Bale, J., Masters, G.J., Hodkinson I., Awmack, C., Bezemer, T.M., Brown, V., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnirnioudis, I., Watt, A.D. & Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1-16.

Basset, Y., Aberlenc, H-P. & Delvere, G. 1992. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology* **17**: 310-318.

Blüthgen, N., Verhaagh, M., Goitía, W., Jaffé, K., Morawetz, W. & Barthlott, W. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia* **125**: 229-240.

Brown, W.L. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. Pp 161-185. *In*, Meggers, B.J., Ayensu, E.S. & Duckworth, W.D. (eds), *Tropical forest ecosystems in Africa and South America: a comparative review.* (Smithsonian Institute Press: Washington).

Bruhl, C.A., Mohamed, M. & Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15**: 265-277.

Coley, P.D. 1980. Effects of leaf age and plant life history patterns on herbivory. *Nature* **284**: 545-546.

Davidson, D.W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of Linnaean Society* **61**: 153-181.

Dejean, A., McKey, D., Gibernau, M. & Belin-Depoux, M. 2000. The arboreal ant mosaic in a Cameroonian rainforest. *Sociobiology* **35**: 403-423.

Fisher, B.L. 1996. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d Andringitra, Madagascar. *Fieldiana. Zoology* (n.s.) **85**: 93-108.

Floren, A., Biun, A. & Linsenmair, K.E. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* **131**: 137-144.

Floren, A. & Linsenmair, K.E. 1997. Diversity and recolonisation dynamics of selected arthropod groups on different tree species in a lowland rain forest in Sabah, Malaysia with special reference to Formicidae. Pp 344-382. *In*, Stork, N.E., Adis, J.A. & Didham, R.K. (eds), *Canopy Arthropods.* (Chapman and Hall: London).

Hölldobler, B. & Wilson, E.O. 1990. *The ants.* (Harvard University Press: Cambridge).

Huxley, C.R. 1982. Ant-epiphytes of Australia. Pp 63-73. *In*, Buckley, R.C. (ed), *Ant-plant interactions in Australia.* R.C. Buckley. (W. Junk Publishers: The Hague).

Gutiérrez, D. & Menéndez, R. 1998. Phenology of butterflies along an altitudinal gradient in northern Spain. *Journal of Zoology, London* **244**: 249-264.

Kitching, R.L., Putland, D., Aston, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55**(2): 271-290.

Lowman, M.D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* **10**: 7-24.

1987. Relationships between leaf growth and holes caused by herbivores. *Australian Journal of Ecology* **12**: 189-191.

Majer, J.D. 1990. The abundance and diversity of arboreal ants in northern Australia. *Biotropica* **22**: 191-199.

Majer, J.D., Kitching, R.L., Heterick, B.E., Hurley, K. & Brennan, K.E.C. 2001. North-south patterns within arboreal ant assemblages from rain forest in eastern Australia. *Biotropica* **33**: 643-661.

Nicholls, N. 2006. Detecting and attributing Australian climate change: a review. *Australian Meteorological Magazine* **55**: 199-211.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., Kasbal, M., Isua, B., Kutil, R., Manumbor, M. & Molem, K. 1999. Predation risk for herbivorous insects on tropical vegetation: a search for enemy-free space and time. *Australian Journal of Ecology* **24**: 477-483.

Olson, D.M. 1992. Rates of predation by ants (Hymenoptera: Formicidae) in the canopy, understory, leaf litter, and edge habitats of a lowland rainforest in southwestern Cameroon. Pp 101-109. *In*, Hallé, F. & Dascal, O. (eds), *Biologie D'une Canopée De Forêt Équatoriale – II. Rapport De Mission: Radeau Des Cimes Octobre Novembre 1991, Réserve De Campo, Cameroun.* (FoundationElf: Paris).

Ødegaard, F. & Diserud, O.H. 2011. Taxonomic composition of Coleoptera, Hemiptera (Heteroptera and Coleorrhyncha) and Mutillidae (Hymenoptera) at five different altitudes in Lamington National Park, (Queensland: Australia). *Memoirs of the Queensland Museum-Nature* **55**(2): 359-374.

Rasband, W. 2003. *ImageJ version 1.31.* (National Institutes of Health: Bethesda).

Reid, C.A.M. 2006. A taxonomic revision of the Australian Chrysomelinae, with a key to the genera (Coleoptera: Chrysomelidae). *Zootaxa* **1292**: 1-119.

SPSS. 2009. *SPSS Version 17, for Windows User Guide.* (SPSS Inc.: Chicago).

Stork, N.E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology* **7**: 161–180.

1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**: 321–337.

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.

Thomas, C.D., Franco, A.M. A. & Hill, J.K. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution* **21**: 415-416.

Tobin, J.E. 1991. A neotropical rainforest canopy, ant community: some ecological considerations. Pp 536-538. *In*, Huxley, C.R. & Cutler, D.F. (eds), *Ant-Plant Interactions.* (Oxford University Press: Oxford).

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389-395.

Plant reproductive phenology and floral resources of an Australian subtropical rainforest

Sarah L. BOULTER

Environmental Futures Centre, Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: s.boulter@griffith.edu.au

William J.F. MCDONALD

Queensland Herbarium, Department of Environment and Resource Management, Mt Coot-tha Rd, Toowong Qld 4066, Australia.

Roger L. KITCHING

Jacinta M. ZALUCKI

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia.

Laurence W. JESSUP

Queensland Herbarium, Department of Environment and Resource Management, Mt Coot-tha Rd, Toowong Qld 4066, Australia.

Citation: Boulter, S.L., McDonald, W.J.F., Kitching, R.L.., Zalucki, J.M. & Jessup, L.W. 2011 12 20: Plant reproductive phenology and floral resources of an Australian subtropical rainforest. *Memoirs of the Queensland Museum – Nature* 55(2): 463-479. Brisbane. ISSN 0079-8835.

ABSTRACT

A survey of the reproductive features of the rainforest flora of Lamington National Park, based on herbarium records and published floras, is presented to provide a community-wide description of floral morphology and flowering phenology. The flora is predominantly composed of shrubs and trees, but also supports a large diversity of vine species. The majority of species (73.5%) have flowers less than 10 mm in diameter of which 80% are white or green in colour. The greatest number of species are in flower from September through to February, although a number of species flower during the cooler, drier winter months. The data compiled on floral features and phenology for individual plant species were assigned to the species lists derived from the IBISCA-Queensland (Qld) altitudinal gradient in Lamington National Park, Australia. No statistically significant changes in flower colour or size were detected with increasing altitude from 300 m to 1100 m a.s.l., but decreasing trends in the proportions of colourful flowers, flowers less than 5 mm in diameter and unisexual flowers were observed. No pollination studies conducted in Lamington National Park have been published although subtropical forests in general are believed to be predominantly generalist pollinated. Data on the morphology of flowers and timing of flowering provide some support for this idea. Determining the prevalence and species turnover of such generalist pollination systems along altitudinal gradients, such as the IBISCA-Qld gradient, could help determine the reproductive resilience of subtropical rainforest plant species under climate change. ❐ *Pollination, flower morphology, phenology, altitudinal gradient, subtropical rainforest.*

The flora of any ecosystem contains a wide range of taxa and a concomitant variety of floral traits. This is especially the case in highly complex rainforest systems. The set of flowering plant species that co-occur within a particular forest or, indeed, within a particular stratum within a forest, presents characteristic ranges and distributions of floral traits. At the community level this is the background against which pollination systems operate. In this paper we describe the basic morphological characteristics and flowering patterns of the flowering plants found in the rainforests of Lamington National Park and associated with the IBISCA-Queensland project (see Kitching *et al.* 2011).

AUSTRALIAN SUBTROPICAL RAINFORESTS

Australian subtropical rainforests are widely distributed along the Australian eastern seaboard, but represent a fraction of land cover area. Webb (1959) described the Australian subtropical rainforests as 'an ecological entity in a broad latitudinal sense'. These subtropical rainforests share many structural and floristic elements with tropical rainforests, but extend geographically well beyond the latitudinal delineation of the tropics (Richards 1996) and are therefore considered a separate formation type. Although quasi-tropical rainforests also exist along the Atlantic coast of Brazil and the northern low and mid-elevation regions of South-east Asia at comparable low latitudes (Richards 1996), these are only partially comparable to the Australian systems (Webb 1959).

Extending from approximately 20°S to about 37°S, the Australian subtropical rainforests represent a number of distinctive features, the most notable of which is the dominance of notophyll leaf sizes amongst the trees (i.e. intermediate between the truly tropical meso- and megaphyll, and the cool temperate microphyll forests; Webb 1959). It is generally supposed that rainforests of this kind dominated a large part of the Australian continent during the Tertiary (Adam 1992), dwindled to a few refuge areas during the last glacial maximum and are now restricted to relatively small discontinuous patches. The present day distribution of subtropical rainforests in Australia results from the interaction of complex rainfall patterns, high altitudes and extant soil types as well as anthropogenic clearing and disturbance (Richards 1996). Floristically, these subtropical rainforests distinguish themselves from their tropical neighbours at the species level (Webb & Tracey 1981) with typical Australian tropical families such as Elaeocarpaceae, Lauraceae and Rutaceae well represented in Australian subtropical rainforests while some of the more abundant species belong to families considered typical of the southern hemisphere such as the Cunoniaceae (Richards 1996). Structurally, these Australian subtropical forests resemble Australian tropical rainforests. The trees reach similar heights and have a comparable presentation of life-forms but with the addition of some more typically temperate groups such as the hemicryptophytes (Richards 1996).

Within the distribution of Australian subtropical rainforests, increasing latitude coincides with a decrease in species diversity and the loss of some tropical characteristics such as cauliflory. The subtropical rainforests of Queensland and New South Wales experience a dry season (five to six months of rainfall less than 100 mm) and a regular and seasonal pattern of substantial temperature variation. As Richards (1996) points out, the coincidence of low temperatures with a dry period, as is the case in Australia's subtropical rainforests, may allow the vegetation to be less affected by water stress than would be the case in seasonal tropical climates. Other microclimatic factors, such as the conditions created by different aspect and topography, also impact on vegetation associations and are important in supporting the survival of subtropical rainforest species.

As with most Australian plant communities (e.g. Boulter *et al.* 2008), there is limited

knowledge of the reproductive systems of these subtropical floras. A collaborative effort to understand these systems by Paul Adam, Geoff Williams and colleagues has contributed a number of significant publications. This includes information on breeding systems (Adam & Williams 2001), wind pollination (Williams & Adam 1999) and the role of insect pollinators (Williams 1995, 1998; Williams & Adam 1995, 2001) in particular thrips (Williams *et al.* 2001). In reviewing pollination in subtropical rainforests, Williams and Adam (1994) identified a number of highly specific plant-pollinator relationships including thrips pollination of *Wilkea hugeliana* (Williams *et al.* 2001), fig-wasp mutualisms in *Ficus* species and weevil-pollination of *Eupomatia laurina* (Williams & Adam 1994). In spite of this, they concluded that generalist pollination is the dominant pollination system, with Diptera, Hymenoptera and Coleoptera the main vectors. The published evidence to support this is limited to very few studies and is largely based on *ad hoc* observations.

The availability and success of individual potential pollinators will depend on each species' (both pollinator and host plant) morphology, breeding system and phenology or life history. The form of these traits in a plant represent a complex response to a number of evolutionary processes including the success of individual pollinator and predator groups (Wyatt 1983), the phylogenetic history of the plant (Johnson & Steiner 2000) and the plasticity of its character traits (Rathcke & Lacey 1985) as well as the changing influence and nature of these factors over evolutionary time (Feinsinger 1983). Knowing something about a plant's morphology and phenology can provide a useful starting point in understanding the reproductive ecology of a flora in the absence of extensive pollinator records and long-term datasets on plant and pollinator phenology.

The primary purpose of this paper is to provide a community-wide description of flower morphology and flowering phenology. In addition we consider the extent to which flower morphology and phenology might change naturally along an altitudinal gradient as part of the IBISCA-Queensland (Qld) project (Kitching *et al.* 2011). At the core of the project has been the establishment of four plots at each of five altitudes at which the vegetation within permanently marked 20 m x 20 m quadrats has been surveyed (Laidlaw *et al.* 2011). We use these vegetation surveys in combination with data sets on morphology and phenology to explore changes in floral landscapes with altitude.

MATERIAL AND METHODS

Study site. Lamington National Park is a large, continuous reserve of predominantly subtropical rainforest approximately 100 km south of Brisbane in southeast Queensland at latitude 28°S. Lamington National Park supports several structural types of subtropical rainforest, including the extensive and dominant type, complex notophyll vine forest (Laidlaw *et al.* 2011; sensu Webb *et al.* 1984) as well as wet sclerophyll forest, open forest and heathlands. The area experiences average annual rainfall totals of 1600 mm, which at times exceed 3000 mm (Bureau of Meteorology Station Number 040182, 'Green Mountains', 917 m a.s.l.), with summer dominated rainfall and dry winter months (July, August and September).

Database construction. A complete list of the vascular plants of Lamington National Park was drawn up using McDonald and Thomas (1990). A total of 1040 species from 148 families are recorded from the park in all vegetation types of which 603 species occur in rainforest vegetation. Of these, 33 species were classified as 'naturalised' (i.e. introduced or exotic) and 81 species as ferns. These were discarded for the analysis, leaving 489 angiosperm plant species for which we built a database of floral morphology characteristics. Information on floral morphology was extracted from existing

TABLE 1. (Opposite page) Flower visitors and pollinators known for subtropical rainforest plant species. Plant species in bold are known to occur in Lamington National Park. Abbreviations for plant growth habits are as follows: E, epiphyte; H, herb, S, shrub, ST, small tree, T, tree; US, understorey shrub; V, vine.

floral treatments and flowering and fruiting phenology using herbarium records and published floras.

Floral Morphology. Information on each species' inflorescence structure and size, individual flower size, colour, shape and scent, reproductive structures, breeding system (e.g. bisexual, dioecious, monoecious) as well as the plants' growth habit and latitudinal and altitudinal ranges were complied using published floral accounts (McDonald & Thomas 1990; Harden 2000; Leiper 2008; Floyd 2008; Botanic Gardens Trust 2009). We assessed photographs and descriptions, where available, to assign a dominant flower colour to each species.

Community-Wide Floral Phenology. A database of the flowering and fruiting phenology for the rainforest species of Lamington National Park was constructed using herbarium specimen records. Records of collection date, altitude, and the latitude and longitude of collection of all specimens recorded as having reproductive structures (i.e. flowers and fruits) were extracted from the Queensland Herbarium's collection database HERBRECS. These records were further filtered for those collected between latitudes 20°S and 37°S to represent collection within the distribution of subtropical rainforests. In addition, we compiled a second list of flowering phenology for each species using published floras (McDonald & Thomas 1990; Harden 2000; Leiper 2008; Floyd 2008; Botanic Gardens Trust 2009) to assign flowering months. From each of these datasets (i.e. herbarium records and published floras) we calculated two measures associated with flowering phenology for each plant species. First, mean flowering times or flowering midpoints were calculated using circular vector statistics (Batschelet 1981; Boulter *et al.* 2006). This was necessary as flowering events for individual species frequently span the calendar break between years, making it inappropriate to use linear models based on a simple numbering of months. Species that flowered in all 12 months or for a discontinuous period were excluded from these calculations. Second, the length of flowering season of each species was calculated. For the data collated from herbarium records, flowering length was calculated as the mean vector length, *r*, as a measure of the concentration of flowering times for each species for which flowering midpoint was calculated (Batschelet 1981). For the information collected from published sources, which was expressed as month(s) of flowering, this was simply a count of the number of months.

IBISCA-QLD Vegetation Survey. All trees greater than or equal to 5 cm diameter at breast height (dbh) were surveyed by staff of the Queensland Herbarium on each of the 20 IBISCA-Qld 20 m x 20 m plots, i.e. four replicate plots at each of five altitudes; 300, 500, 700, 900 and 1100 m a.s.l. In addition all species found in the understorey of each plot were recorded. The complete survey methodology and results are described in Laidlaw *et al.* (2011). We used the data from the herbarium surveys to construct a species list for each plot at each altitude and, using the morphology and phenology databases we had prepared, collated flower morphology and phenology characteristics for each altitude.

Analyses. Estimates of flowering season length and mid-flowering peak using both the herbarium data and information derived from published floras were used to determine if the two sources of data provided comparable patterns. The first estimate, flowering midpoint was circular and was compared using a circular correlation analysis (Batschelet 1981). The second estimate – flowering season length – was linear and we compared these using a paired *t*-test.

Plant Family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
ANACHARDIACEAE									
Euroschinus falcata	T	Bisexual or dioecious	Cream	6 mm	Dish	N/A	bees; *Glycyphana brunnipes* (Scarabaeidae: Cetoniinae); *Polistes humilis* (Hymenoptera: Vespidae); *Myrmecia nigrocincta* (Hymenoptera: Formicidae); *Amata* sp. (Lepidoptera: Arctiidae); *Apis mellifera*; *Castiarina producta* (Coleoptera: Buprestidae)	Subtropical rainforest, NSW	Williams 1995
ATHEROSPERMATACEAE									
Daphnandra micrantha	ST	Bisexual	White/ Green	8 mm	Dish	Nematocera?		Riparian rainforest, Lorien Wildlife Refuge, NSW	Williams 1995
COMMELINACEAE									
Pollia crispata	H	Bisexual	White	10 mm	Open/ Dish		Syrphid flies, halictid bees, *Trigonia carbonaria*	Subtropical rainforest, Lorien Wildlife Refuge, NSW	Williams & Walker 2003
CUNONIIACEAE									
Davidsonia johnsonii	T	Bisexual	Pink	7 mm	Dish	unknown	bees (native included), beetles and ants	Subtropical rainforest, NSW	Department of Environment and Conservation NSW 2004
EBENACEAE									
Diospyros australis	S/T	Dioecious	Cream	5 mm	Tube		bees - Anthophoridae, *Hylaeus ?primulipictus*	Subtropical rainforest, NSW	Williams 1995
EUPOMATIACEAE									
Eupomatia bennetti	S	Bisexual	Yellow	25 mm	Complex structure	*Elleschodes* spp. (weevils)		Subtropical rainforest, NSW	Endress 2003
Eupomatia laurina	S/T	Bisexual	White	20 mm	Complex structure	*Elleschodes* spp. (weevils)	ptiliid beetle, cockroach, thrips	Subtropical rainforest, NSW	Endress 2003; Williams & Adam 1994 and various references cited therein
FABACEAE									
Senna acclinis	S	Bisexual	Yellow	?	Cup-shaped	*Amphylaeus nubilosellus, Hylaeus turgicollaris, Lasioglossum polygoni*	diverse assemblage of native bees	Littoral rainforest, Halidays Point, NSW	Williams 1998
LAURACEAE									
Neolitsea dealbata	T	Dioecious	Cream	2 mm	Tube		Coleoptera, Hymenoptera, Diptera	Tropical rainforest	House 1985, 1989

TABLE 1. cont...

Plant Family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
MONIMIACEAE									
Wilkiea huegeliana	S/T	Dioecious	Cream	3 mm	Urceolate	Thrips setipennis	*Trigona carbonaria* (Apidae) ?*Crematogaster* and *Camponotus* ants	Subtropical rainforest, NSW	Williams 1995
MORACEAE									
Ficus macrophylla	T	Monoecious	Orange	22.5 mm	Fig	Pleistodontes froggatti			Lopez-Vaamonde et al. 2002
Ficus obliqua	T	Monoecious	Orange	9 mm	Fig	*Pleistodontes greenwoodi; Pleistodontes xanthocephalous*			Lopez-Vaamonde et al. 2002; Dixon et al. 2001
Ficus rubiginosa	T	Monoecious	Yellow	15 mm	Fig	*Pleistodontes imperialis*			Lopez-Vaamonde et al. 2002; Dixon et al. 2001
Ficus watkinsiana	T	Monoecious	Purple/ Black	30 mm	Fig	*Pleistodontes nigriventris*			Lopez-Vaamonde et al. 2002
Maclura cochinchinensis	V	Dioecious	Yellow	1 mm	Inflorescence: Globulose head	thrips		Subtropical rainforest, NSW	Williams et al. 2001
Streblus brunonianus	T	Dioecious	Cream	4 mm	Dish	facultatively wind pollinated		Subtropical rainforest, NSW	Williams & Adam 1993
MYRSINACEAE									
Rapanea howittiana	S/T	Bisexual	Cream	3 mm	Closed; fused perianth	thrips		Riverine rainforest, Landsdowne Reserve, NSW	Williams 1995
Rapanea subsessilis	US	Gynodioecious	Cream	3 mm	Closed; fused perianth	thrips	*Trigona* sp.; thrips	Tropical rainforest	Harrison 1987; Jackes 2005
Rapanea variabilis	S/T	Bisexual	Cream	2 mm	Closed; fused perianth	thrips		Subtropical rainforest, NSW	Williams 1995
MYRTACEAE									
Acmena smithii	T	Bisexual	Cream	7 mm	Cup-shaped		bees	Littoral rainforest, Harrington, NSW	Williams 1995
Tristaniopsis laurina	T	Bisexual	Yellow	10 mm	Dish		bees	Subtropical rainforest, NSW	Williams 1995

TABLE 1. cont...

Plant Family and species	Habit	Sexual system	Flower colour	Flower diameter	Flower shape	Pollinators	Flower visitors	Habitat/location sampled	Source
Waterhousea floribunda	T	Bisexual	White	3 mm	Cup-shaped		bees	Subtropical rainforest, NSW	Williams 1995
ORCHIDACEAE *Dendrobium monophyllum*	E	Bisexual	Yellow	10 mm	Orchidaceous	*Trigona*		Herberton, Atherton Tablelands-Tropical rainforest	Bartareau 1993
PROTEACEAE *Hicksbeachia pinnatifolia*	S/T	Bisexual	Pink	15 mm	Tube		Native & introduced bees, moths None seen to contact pollen presenter	Lismore, NSW	Goldingay & Bowen 2003
Triunia youngiana	S	Bisexual	White/pink	15 mm	Tube		Butterflies & moths (contacted pollen presenter) Flies, ants & beetles (no contact with pollen presenter)	Lismore, NSW	Goldingay & Bowen 2003
RHAMNACEAE *Alphitonia excelsa*	T	Bisexual	White	4.5 mm	Dish		bees	Littoral rainforest, Harrington, NSW	Williams 1995
ROUSSEACEAE *Cuttsia viburnea*	S/T	Bisexual	White	4 mm	Dish		Colletidae-Colletinae (*?Leioproctus*)	Subtropical rainforest, Lorien Wildlife Refuge, NSW	Williams 1995
RUTACEAE *Acradenia euodiiformis*	S	Bisexual	White	8 mm	Dish		bees	Subtropical rainforest, NSW	Williams 1995
SAPINDACEAE *Alectryon coriaceus*	S/T	Monoecious	White	2 mm	Cup-shaped	Facultatively ant-pollinated?	bees	Littoral rainforest, Harrington, NSW	Williams 1995
Guioa semiglauca	T	Monoecious/dioecious	Cream	3 mm	Dish		bees, *Apis mellifera, Phyllotocus australis* (Scarabaeidae)	Littoral rainforest, Harrington, NSW	Williams 1995
SMILACACEAE *Smilax glyciphylla*	V	Dioecious	White	4 mm	Cup-shaped	thrips		Subtropical rainforest, NSW	Williams 1995
VITACEAE *Cissus antarctica*	V	Bisexual	Yellow	5 mm	Dish	generalist		Subtropical rainforest, NSW	Williams 1995

The statistical significance of associations between flower colour, habit and flower size were tested using chi squared analyses. The association between altitude and different proportions of habit, flower colour and category of flower size were also tested using chi squared analyses.

RESULTS

Whole Flora

Habit. Of the 570 plant species found in the rainforests of Lamington National Park, approximately 21% are trees, 23% shrubs and a further 7% can take the form of either a small tree or a tall shrub (Fig. 1). Vines made up about 14% of the total, as did ferns. Other life forms included forbs (7%), epiphytes (7%), graminoids (3.5%) and parasites (i.e. mistletoes) (1%).

Flower size. Floral diameter could be determined for 448 plant species, with almost three quarters (73.7%) having flowers less than 10 mm in diameter. Fewer than 10% of plants had flowers greater than 20 mm in diameter. The distribution of flower sizes appeared more or less uniform across all growth habits with the exception of parasites (Fig. 1) with no significant relationship between the two variables ($c^2 = 24.78$, d.f. = 21, $P = 0.26$).

Flower colour. Dominant flower colour was determined for 350 of the target species which were grouped into the following categories: white/green, yellow/orange, pink/red, blue/purple and brown. These groupings were based on colour groups generally associated with pollination syndromes (e.g. red or pink associated with bird pollination syndromes (Faegri & van der Pijl 1979)). The overwhelming majority of flowers were white/green (73%). Of the remaining species, 12.5% have yellow/orange flowers, 6% pink/red, 6% blue/purple and 2% brown. When we considered the proportional representation of flower colour groups within each plant growth habit type (Fig. 2), not surprisingly, white/green flowers dominated across all types. There was a strong association between colour and habit type ($c^2 = 170.11$, d.f. = 28, $P < 0.0001$), largely due to the colour bias in graminoids and parasites. When these were omitted from the analysis there was no significant association ($c^2 = 9.6$, d.f. = 12, $P = 0.65$). Flower size and colour showed a clear association ($c^2 = 36.69$, d.f. = 12, $P = 0.0003$). The proportion of white/green flowers decreased with increasing flower size (Fig. 3) with small flowers more often a dull white or green colour and large flowers more often colourful.

Sexual Systems. Most plant species in the Lamington rainforests are bisexual (ca. 67%, n = 479). Most of the remainder of species have unisexual flowers although about 5% can have both bisexual and unisexual flowers (e.g. Asteraceae). Of the 127 unisexual species, more than half (n = 71) are monoecious.

Phenology. Preliminary analysis showed good congruence between flowering estimates derived from herbarium data and those derived from published floras. There was a strong positive correlation between flowering midpoints derived from the two data sources ($R_+ = 0.49$, $P<0.001$, n = 393), suggesting that the herbarium records provided a reliable basis on which to assess the flowering times of species. In contrast, the independent assessments of flowering season length differed slightly (paired $t = 1.83$, $P = 0.06$). Flowering season length averaged 5.58 and 5.26 months for the herbarium records and published flora data respectively. This suggests that the herbarium records overestimate flowering season compared to published floras. This may reflect the fact that the herbarium records were collected across the entire distribution of subtropical rainforests, while published floras may be based more on local records and knowledge. For the rest of the analyses, we used the data derived from the herbarium collections.

All surveyed species from Lamington National Park showed distinct seasonality in their flowering patterns with most flowering in November

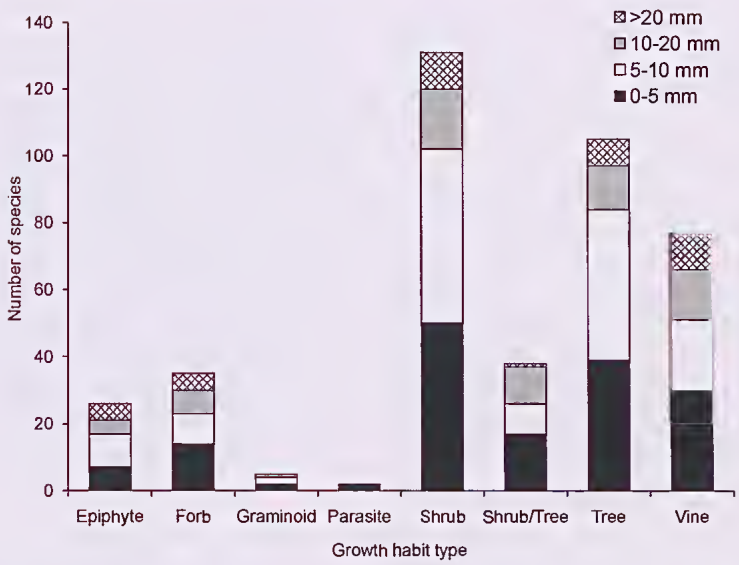


FIG. 1. Number of species in each of four flower diameter size classes within growth habit types for angiosperm species found in the rainforests of Lamington National Park.

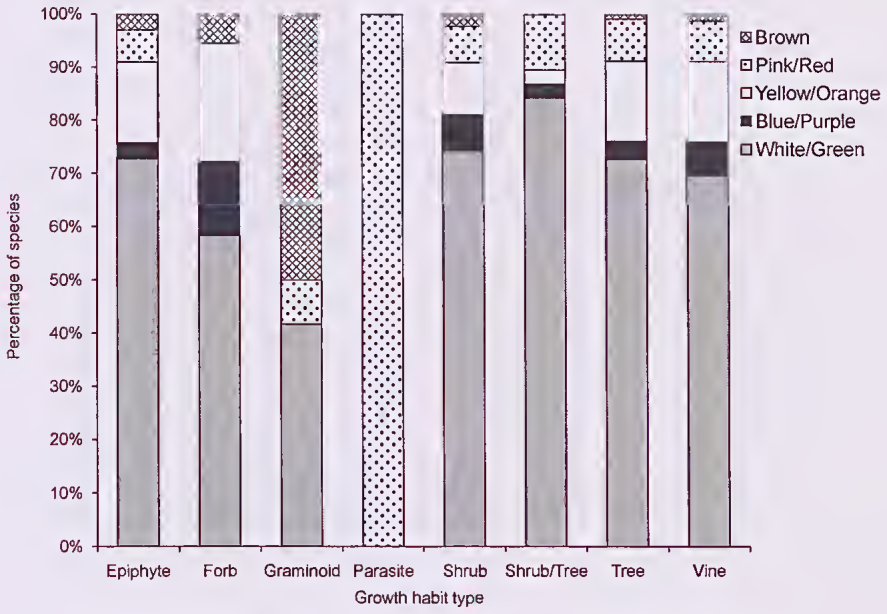


FIG. 2. Proportions of Lamington National Park rainforest species displaying different flower colours within eight different plant growth habit types. See figure 1 for the number of plant species within each habit type.

(n = 285) and December (n = 287) and the least in June (n = 129) and July (n = 125). Using the calculated flowering peak for all species, flowering activity is clearly at its most intense around November (Fig. 4).

Changes in Floral Morphology with Alititude

Including both understorey and tree species, the twenty IBISCA-Qld vegetation plots (situated between 248 m a.s.l. and 1142 m a.s.l.) contained a total of 287 plant species from 82 families. Looking at the total number of species recorded at each altitude (Fig. 5), there was a clear decrease in diversity with increasing altitude. At the 900 m and 1100 m altitudes this appeared to coincide with a decrease in the number of tree species, fern species and the absence of forb species (Fig. 5). However, of note is that species classified as graminoids were present at higher altitudes and included *Drymophila moorei* which was only found at the 1100 m altitude plots. No epiphyte species were recorded at the 300 m sites. However the proportion of each plant habit type was not dependent on altitude (χ^2 = 22.07, d.f. = 28, P = 0.78). The proportion of species with flowers less than 5 mm in diameter appeared to decrease slightly with increasing altitude (Fig. 6) but no significant statistical relationship was detected between flower size and altitude (χ^2 = 7.74, d.f. =12, P = 0.80). While no significant association between flower colour and altitude was detected (χ^2 = 6.78, d.f. =16, P = 0.98) there appeared to be an increase in the proportion of species with white/green flowers, and a decease in the proportion of yellow flowers, the higher along the altitudinal gradient we sampled (Fig. 7).

The proportion of bisexual and dioecious species appeared to increase with increasing altitude (Fig. 8) although neither showed a statistically significant relationship with altitude (bisexuality vs altitude, χ^2 = 14.74, d.f. =8, P = 0.07; dioecy vs altitude, χ^2 = 10.54, d.f. =8, P = 0.22).

Using flowering midpoints derived from herbarium specimens to determine average flowering patterns for the species present at each of the IBISCA-Qld altitudes, it can be seen that the proportion of species flowering in any given month (Figure 9) is highly seasonal at all altitudes. The seasonal pattern is more or less consistent across all altitudes with a dramatic increase in flowering starting in August and maintenance of this level of activity until February. A chi square test demonstrated there was no significant difference in the pattern of flowering between altitudes (χ^2 = 17.8, d.f. = 44, P = 0.99). Repeating the analysis on low altitude (300, 500 and 700 m a.s.l.) and high altitude (900 and 1100 m a.s.l.) data sets, again no significant association was found between the number of species flowering and altitude (χ^2 = 5.63, d.f. = 11, P = 0.90).

DISCUSSION

Our results are of interest from three perspectives. First those that relate to the Lamington rainforest flora as a whole, second, those that quantify altitudinal trends, and third, those which can be used to erect hypotheses about likely pollinators and pollination syndromes. The first is useful in understanding the floral landscape of the Lamington rainforests. The second addresses the impacts of closely adjacent climates upon floral biology and is relevant to predicting likely impacts of climate change. The third, concerning pollination, is most useful in informing future, focussed studies and will be relevant to both spatial comparisons and in predicting future changes of pollination in subtropical rainforests.

The Lamington Rainforest as a whole. Small, white or green flowers dominate the Lamington flora with, as would be expected, the majority bisexual. Small, dull-coloured, simple flowers are often associated with generalist pollination systems (Faegri & van der Pijl 1979). Williams and Adam (1994) suggested that generalist pollination (defined in this case as having pollinators drawn from a wide range of small insects) prevails in subtropical rainforest

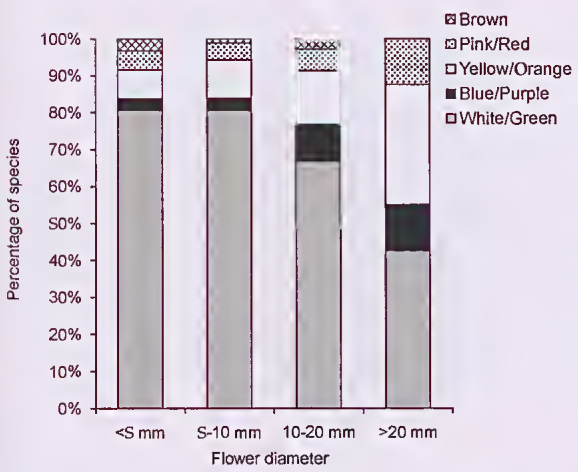


FIG. 3. Proportions of Lamington National Park rainforest species displaying different flower colours within four different classes of flower diameter.

systems and this is associated with a dominance of unspecialised flower structures. As flowers become larger they also become more colourful with flowers greater than 10 mm in diameter displaying more colour than their smaller counterparts. About a third of the species in the Lamington rainforests for which information was available (109 species out of 350) had flowers greater than 10 mm in diameter, and of those 109 species, more than 40% were a colour other than white or green. Families with a number of species with large, coloured flowers were Orchidaceae (6 spp.), Fabaceae (6 spp.), Moraceae (5 spp.), Solanaceae (4 spp.) and Asteraceae (4 spp.) all of which also include species with smaller, non-colourful flowers with the exception of Fabaceae. This suggests that the incidence of large, colourful flowers may not necessarily be phylogentically constrained. Larger, more colourful flowers are generally associated with bird, butterfly and beetle pollination (Faegri & van der Pijl 1979), although the attraction of pollinators to

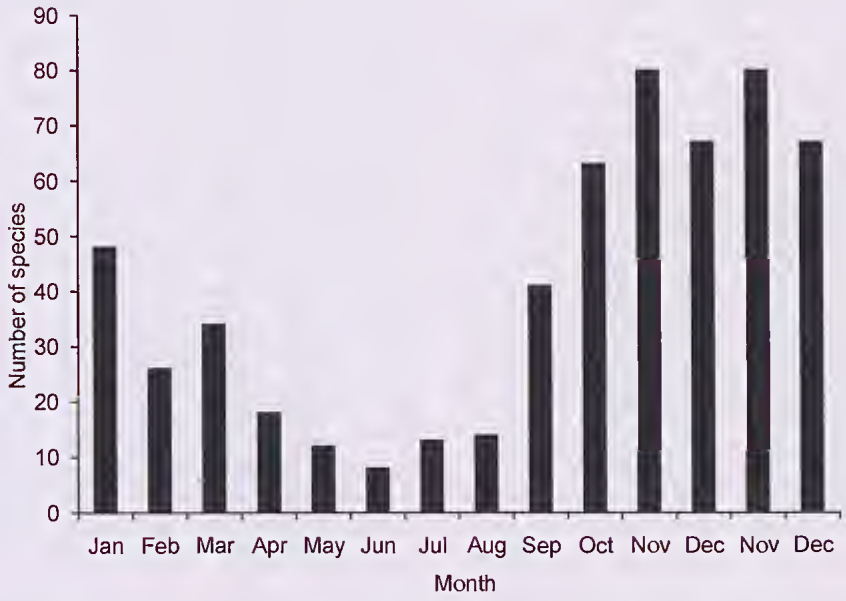


FIG. 4. The distribution of mean flowering times ('peak' flowering) for all species of angiosperm known from the rainforests of Lamington National Park derived from herbarium collections between 20°S and 37°S.

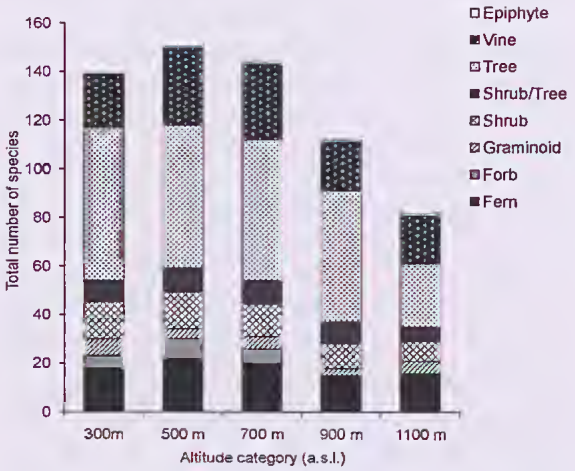


FIG. 5. Total number of vascular plant species, classified according to their growth habit types, recorded from all four replicate plots across the five IBISCA-Qld altitude categories (m a.s.l.).

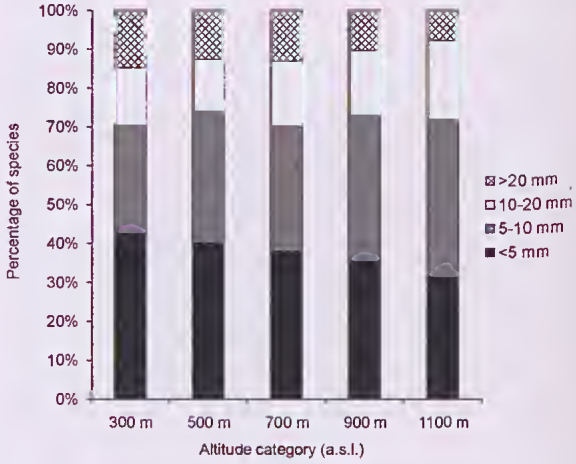


FIG. 6. Proportions of plant species in each of four flower size categories, across the five IBISCA-Qld altitude categories (m a.s.l.).

the flowers of particular species is also related to other attractants like scent, and the success of pollination will depend on more complex morphological characteristics such as flower shape and the position of reproductive structures. Flower colour was strongly related to growth habit for parasites, graminoids and forbs. All five species of parasites, from two families, have red flowers. Brightly coloured flowers are common in species from these families (Loranthaceae and Viscaceae) and have been associated with bird pollinators. Among the graminoids, mainly consisting of members of the families Cyperaceae and Poaceae, flowers were found to be white, green or brown with the exception of the spectacular pink flowers of *Helmholtzia glaberrima* (J.D. Hook) Caruel (Philydraceae).

A strong seasonal pattern of flowering was demonstrated in the rainforest of Lamington National Park at the scale of analysis presented here. Dramatic increases in the number of species in flower occur from around September with the greatest flowering activity in November, coinciding with the end of an extended dry period and start of the wet season (Strong *et al.* 2011). Flowering is frequently influenced by rainfall and it is likely that flowering in many of the Lamington subtropical rainforest species is in response to proximate environmental cues. Seasonal cues other than rainfall include day length and temperature, and individual species are likely to respond differentially to different cues. This seasonal flowering activity is likely to coincide with the seasonal activity of pollinator insect species. A considerable number of plant species flower outside of this peak flowering time and these may represent species that have been influenced by different selection pressures to those experienced by other species. Flowering during cooler periods equates to a lower availability and diversity of pollinators (Williams & Adam 1994). This might suggest avoidance of a detrimental pressure (e.g. conspecific competition for pollinators) that outweighs flowering to optimise pollinator visitation, i.e. flowering during the peak pollinator activity season.

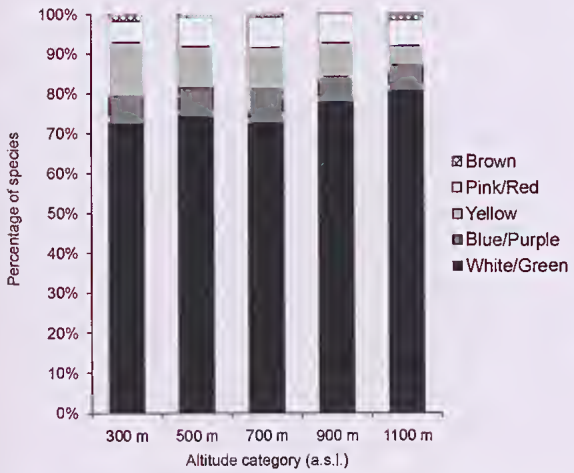


FIG. 7. Proportions of plant species in five dominant flower colour categories, across the five IBISCA-Qld altitude categories (m a.s.l.).

Altitudinal Changes. By global standards the IBISCA-Qld Lamington transect is a rather short one, spanning an altitudinal range of just 800 vertical metres (Beck *et al.* 2008). Accordingly, although we might hope to identify clear trends, the low magnitude of altitudinal change along the transect mitigates against dramatic contrasts. In addition, here we have measured averages (e.g. average flowering period rather than actual first flowering date) across species and so proximate responses to microclimatic cues could not be detected. However, given that patterns of flowering phenology (Boulter *et al.* 2006) and pollinator movements (Torres-Diaz *et al.* 2007) are driven by climatic cues, we would expect that the microclimatic variation along the altitudinal gradient would give rise to variation in pollination systems. Whether this has translated into different floral morphologies is more difficult to determine and our data have not provided conclusive evidence to support this supposition.

Although not statistically significant, some trends were apparent, even along this short altitudinal gradient: more 'medium'-sized flowers (and less tiny and large flowers), more dull-coloured flowers and less yellow flowers, more bisexual flowers and increase in the likelihood of species with unisexual flowers to be dioecious with increasing altitude. Field-based studies are required to confirm these trends, but they present some possible support for the notion

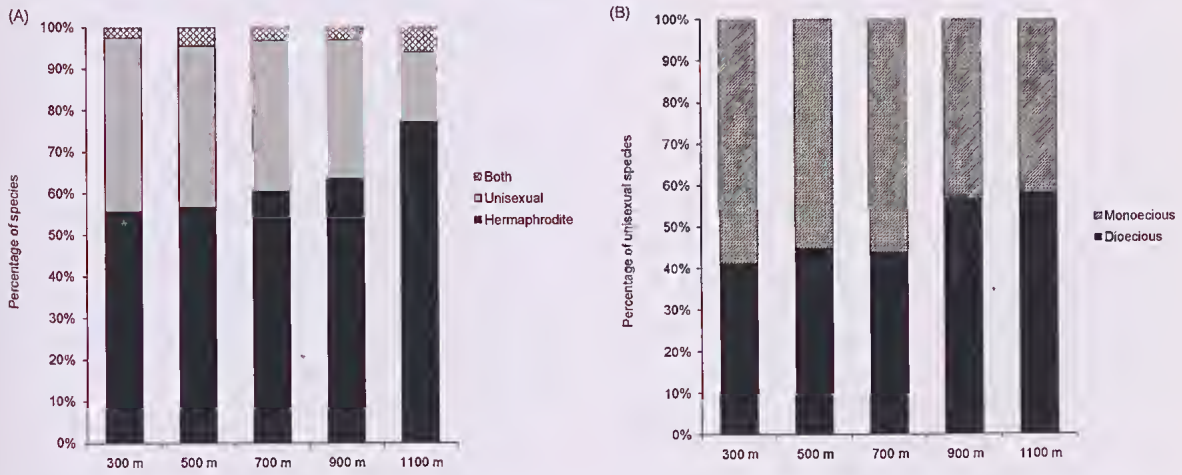


FIG. 8. Proportions of (a) plant species with different breeding systems and (b) plant species with unisexual flowers showing dioecy or monecy, across the five IBISCA-Qld altitude categories (m a.s.l.).

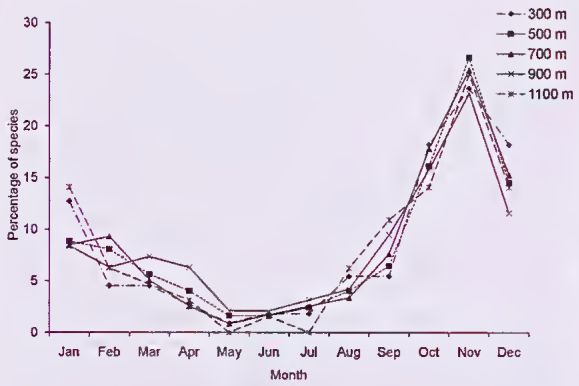


FIG. 9. Percentage of angiosperm species in peak flowering in each month of the year, based on flowering midpoint calculated from herbarium records, within each of the five IBISCA-Qld altitude categories (m a.s.l.).

that the floral display at higher altitudes might be a response to a reduction in available pollinators. Floral traits have been shown to be under selection pressure from pollinators (Waser 1983) and as a result these flower traits have been traditionally thought to demonstrate a significant association with the dominant pollinator of the plant species, i.e. the pollination syndrome concept. With increasing altitude we would expect a decrease in the abundance and diversity of some insect groups in general, with some less able to function at higher altitudes. As a result, the dominant pollinator groups will change with increasing altitude. Generally, a decreasing number of plants are pollinated by Hymenoptera with increasing altitude, whereas Lepidoptera and Diptera in particular, are increasingly important pollinators along the same gradients (Warren *et al.* 1988; Arroyo *et al.* 1982; Kearns 1992). Previous studies have found more blue flowers in upland sites (Weevers 1952), higher proportions of, and increased visitation to, white and yellow flowers (reviewed in Arnold *et al.* 2009). However, Arnold *et al.* (2009) did not find a relationship between altitude and flower colour according to ecologically relevant models of insect vision (as opposed to human perception of colour).

Likely pollinators and pollination syndromes. As already highlighted, the subtropical rainforests of Australia are considered to be dominated by generalist pollination systems (Williams & Adam 1994). These systems are usually characterised by white or dull-coloured flowers with simple, general flower structures (e.g. bowl or dish-shaped flowers). Under the pollinator syndrome concept, white or dull-coloured flowers are usually associated with beetles, flies, non-specialised bees, moths, bats and thrips (Ollerton & Watts 2000). Based on the pollination syndrome concept then, we might conclude, that over seventy percent of the flowers in the subtropical rainforest of Lamington National Park should be visited by these groups. The distinction between flower types matching each of these pollinator groups generally comes down to flower structure, scent and anthesis. So for example, a night flowering species with a white, musky-odoured, brush-like flower would be associated with bats. Coloured flowers are more often associated with butterflies, bees, birds and other vertebrates. However, caution must be exercised in relying too heavily on flower colour as an indication of likely pollinators, as the success of a flower visitor also relates to their behaviour, the structure of the flower, the presence and accessibility of rewards and so on. The traditional pollinator syndrome should be used with caution when interpreting floral diversity or inferring pollinators, as a recent test of the concept has shown limited match between predicted and actual pollinators (Ollerton *et al.* 2009). Ollerton *et al.* (2009) suggest that rather than abandoning the concept of pollination syndromes, how traits of flowers and pollinators relate to visitation and pollen transfer needs reconsidering to determine if a new categorisation of floral functional diversity can be more successfully used than the traditional syndromes.

To date there have been no published studies of pollination conducted in Lamington National Park. However, the flower visitors and pollinators of 27 plant species that are found in Lamington National Park have been studied in

other locations (Table 1). A further five plant species found in subtropical rainforests, but not in Lamington, have had pollinators or flower visitors identified (Table 1). Of these 33 plant species, 18 have a named pollinator species or group of taxa. Only one was described as having a generalist pollination system, although many of the plants with only flower visitors recorded may, in fact, have generalist pollinators e.g. *Euroschinus falcata* which is visited by a number of different insect orders. The identification of Nematocera, a large and diverse group of primitive flies, as pollinators of *Daphnandra micrantha* may also suggest a general pollination system in this plant species. However, the overwhelming majority of reported studies describe specialised pollination, in that a single species or closely related taxa are identified as pollinators. We would suggest that this presents a biased picture of the dominant pollination system in subtropical rainforests, as these studies were all made on plants with complex flower structures not suited to a wide variety of pollinators.

CONCLUSIONS

This study provides a broad overview of the general floral morphology and phenology of the subtropical rainforest flora of Lamington National Park. In addition, a preliminary exploration of the variety of these characteristics among plant species at different altitudes was undertaken. A search of the pollination literature revealed that very little is known about the pollinators of, and flower visitors to the plant species of subtropical rainforests. Variation of flower morphologies found at different altitudes could have implications for the identity of different effective pollinators. If the dominance of specialised interactions seen in the literature reflects that of the flora as a whole, then these systems maybe more vulnerable to changes in climate, with the uncoupling of mutualistic interactions a key threat. However, if subtropical rainforest plants are indeed predominantly generalist pollinated as suggested by Williams and Adam (1994) and with some support from our own findings, then this might confer these forests with a degree of reproductive robustness under a changing climate. Altitudinal studies of changes in flower visitors and pollinator assemblages to plant species identified as potentially generalist could help determine the resilience of these systems under different climate conditions.

A study of the type presented here, provides an opportunity to gain a broad understanding of a flora and its phenology and reproduction in the absence of fine-scale studies that would take many years of effort to achieve. However, the information derived at this scale cannot reveal many of the intricate and complex interactions between plant species and their pollinators in Lamington National Park. A limitation of this type of study is an inability to demonstrate site specific characteristics e.g. phenology of individual species across altitudes, and more detailed studies are essential in order to better understand the reproductive functioning of subtropical rainforests.

ACKNOWLEDGEMENTS

We thank Dr Chris Burwell for comments on an early draft of the manuscript, which greatly improved the final paper. S.B. was the grateful recipient of a Queensland government Smart State grant during the preparation of this manuscript. This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the

federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort.

LITERATURE CITED

Adam, P. 1992. *Australian Rainforests.* (Oxford University Press: New York).

Adam, P. & Williams, G. 2001. Dioecy, self-compatability and vegetative reproduction in Australian subtropical rainforest trees and shrubs. *Cunninghamia* **7**: 89-100.

Arnold, S.E.J., Savolainen, V. & Chittka, L. 2009. Flower colours along an alpine altitude gradient, seen through the eyes of fly and bee pollinators. *Arthropod-Plant Interactions* **3**: 27-43.

Arroyo, M.T., Primack, R. & Armesto, J.J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany* **69**: 82-97.

Bartareau, T.M. 1993. *The Reproductive Ecology and Biology of Eight Orchid Species Endemic in North-East Queensland.* MSc thesis, James Cook University.

Batschelet, E. 1981. *Circular Statistics in Biology.* (Academic Press Inc.: London).

Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. 2008. *Gradients in a Tropical Mountain Ecosystem of Ecuador.* (Springer-Verlag: Berlin Heidelberg).

Botanic Gardens Trust. 2009. PlantNET - The Plant Information Network System of Botanic Gardens Trust. Version 2.0. Sydney, Australia.

Boulter, S.L., Kitching, R.L. & Howlett, B.G. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology* **94**: 369-382.

Department of Environment and Conservation. 2004. Recovery plan for *Davidsonia johnsonii* (Smooth Davidsonia). (Department of Environment and Conservation: Hurstville, NSW).

Dixon, D.J., Jackes, B.R. & Bielig, L.M. 2001. Figuring out the figs: the *Ficus obliqua-Ficus rubiginosa* complex (Moraceae: *Urostigma* sect. *Malvanthera*). *Australian Systematic Botany*, **14**: 133-154.

Endress, P.K. 2003. Early floral development and nature of the calyptra in Eupomatiaceae (Magnoliales). *International Journal of Plant Science* **164**: 489-503.

Faegri, K. & van der Pijl, L. 1979. *The Principles of Pollination Ecology.* (Pergamon Press: Oxford, New York).

Feinsinger, P. 1983. Coevolution and pollination. Pp. 283-210. *In,* Futuyama, D.J. & Slatkin, M. (eds), *Coevolution.* (Sinauer Associates Inc.: Sunderland).

Floyd, A.G. 2008. *Rainforest Trees of Mainland South-Eastern Australia.* (Terania Rainforest Publishing: Lismore).

Goldingay, R. & Bowen, M. 2003. The breeding systems of *Hicksbeachia pinnatifolia* and *Triunia youngiana* (Proteaceae). *Cunninghamia* **8**: 157-161.

Harden, G.J. 2000. *Flora of New South Wales.* (NSW University Press: Kensington).

Harrison, K. 1987. *Floral biology of three tropical Australian species* Aegiceras corniculatum, Maesa dependens *and* Rapanea subsessilis *(Myrsinaceae).* BSc Hons thesis, James Cook University.

House, S.M. 1985. *Relationships between breeding and spatial pattern in some dioecious tropical rainforest trees.* PhD thesis, Australian National University.

House, S.M. 1989. Pollen movement to flowering canopies of pistillate individuals of three rain forest tree species in tropical Australia. *Australian Journal of Ecology* **14**: 77-94.

Jackes, B.R. 2005. Revision of *Myrsine* (Myrsinaceae) in Australia. *Australian Systematic Botany* **18**: 399-438.

Johnson, S.D. & Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology and Evolution* **15**: 140-143.

Kearns, C.A. 1992. Anthophilous fly distribution across an elevation gradient. *American Midland Naturalist* **127**: 172-182.

Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* 55(2): 235-250.

Laidlaw, M.J., McDonald, W.J.F., Hunter, J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradsect. *Memoirs of the Queensland Museum-Nature* 55(2): 271-290.

Leiper, G. 2008. *Mangroves to Mountains: A Field Guide to the Native Plants of South-east Queensland.* (Society for Growing Australian Plants (Qld Region): Logan River Branch, Browns Plains, Qld).

Lopez-Vaamonde, C., Dixon, D.J., Cook, J.M. & Rasplus, J. 2002. Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host-plant association. *Zoological Journal of the Linnean Society* **136**: 637-683.

McDonald, W.J.F. & Thomas, M.B. 1990. *The Flora of Lamington National Park : A Preliminary Checklist*

of the Vascular Plant Species. (Dept. of Primary Industries, Queensland Government: Brisbane).

Ollerton, J., Alarcon, R., Waser, N.M., Price, M.V., Watts, S., Cranmer, L., Hingston, A., Peter, C.I. & Rotenberry, J. 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**: 1471-1480.

Ollerton, J. & Watts, S. 2000. Phenotype space and floral typology: towards an objective assessment of pollination syndromes. Pp. 149-159. *In*, Totland, Ø., Armbruster, W.S., Fenster, C., Molau, U., Nilsson, L.A., Olesen, J.M., Ollerton, J., Philipp, M. & Ågren, J. (eds), *Scandinavian Association for Pollination Ecology Honours Knut Fægri*. (Norwegian Academy of Science and Letters 39: Oslo).

Rathcke, B.J. & Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179-214.

Richards, P.W. 1996. *The Tropical Rain Forest*. (Cambridge University Press: Cambridge).

Strong, C.L., Boulter, S.L., Laidlaw, M.J., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* 55(2): 251-270.

Torres-Diaz, C., Cavieres, L.A., Munoz-Ramirez, C. & Arroyoz, M.T.K. 2007. Consequences of microclimate variation on insect pollinator visitation in two species of *Chaetanthera* (Asteraceae) in the central Chilean Andes. *Revista Chilena De Historia Natural* **80**: 455-468.

Warren, S.D., Harper, K.T. & Booth, G.M. 1988. Elevational distribution of insect pollinators. *American Midland Naturalist* **120**: 325-330.

Waser, N.M. 1983. The adaptive nature of floral traits: ideas and evidence. Pp. 241-285. *In*, Real, L. (ed.), *Pollination Biology*. (Academic Press: London).

Webb, L.J. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology* 47: 551-570.

Webb, L.J. & Tracey, J.G. 1981. Australian rainforests: patterns and change. Pp. 605-694. *In*, Keast, A. (ed.), *Ecological Biogeography of Australia*, (Junk: The Hague).

Webb, L.J., Tracey, J.G. & Williams, W.T. 1984. A floristic framework of Australian rainforests. *Australian Journal of Ecology* 9: 169-198.

Weevers, T. 1952. Flower colours and their frequency. *Acta Botanica Neerlandica* **1**: 81-92.

Williams, G. 1995. *Pollination Ecology of Lowland Subtropical Rainforests in New South Wales*. PhD thesis, The University of New South Wales, Sydney.

1998. Bee pollination in the threatened Australian shrub *Senna acclinis* (Ceasalpinioideae). *Cunninghamia* 5: 767-772.

Williams, G. & Adam, P. 1993. Ballistic pollen release in Australian members of the Moraceae. *Biotropica* **25**: 478-480.

1994. A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests. *Australian Zoologis* **29**: 177-212.

1995. Records of aculeate wasps from flowering subtropical rainforest trees. *Australian Entomologist* **22**: 51-58.

1999. Pollen sculpture in subtropical rain forest plants: is wind pollination more common than previously suspected? *Biotropica* **31**: 520-524.

2001. The insect assemblage visiting the flowers of the subtropical rainforest pioneer tree *Alphitonia excelsa* (Fenzl) Reiss. ex Benth. (Rhamnaceae). *Proceedings of the Linnean Society of New South Wales* **123**: 235-259.

Williams, G.A., Adam, P. & Mounds, L.A. 2001. Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of *Wilkiea huegeliana* (Monimiaceae). *Journal of Natural History* 35: 1-21.

Williams, G. & Walker, K. 2003. Pollination of the wet forest herb *Pollia crispata* (Commelinaceae). *Cunninghamia* 8: 141-146.

Wyatt, R. 1983. Pollinator-plant interactions and the evolution of breeding systems. Pp. 51-95. *In*, Real, L. (ed.), *Pollination Biology*. (Academic Press Inc.: Orlando).

Vegetation traits and herbivory distribution in an Australian subtropical forest

Sérvio P. RIBEIRO

Milton Barbosa DA SILVA Jr.

Marcela Cezar TAGLIATI

Laboratory Evolutionary Ecology of Canopy Insects, Department of Biodiversity, Evolution and Environment/ICEB/Universidade Federal de Ouro Preto, Ouro Preto, MG, Brazil. Email: spribeiro@iceb.ufop.br

Cecilia CHAVANA-BRYANT

Environmental Change Institute, University of Oxford, Oxford, United Kingdom.

Citation: Ribeiro, S.P., Da Silva, M.B. Jr., Tagliati, M.C. & Chavana-Bryant, C. 2011 12 20: Vegetation traits and herbivory distribution in an Australian subtropical forest. *Memoirs of the Queensland Museum – Nature* 55(2): 481-493. Brisbane. ISSN 0079-8835.

ABSTRACT

We tested the hypothesis that leaves in the canopy should have higher sclerophylly indices compared with understorey leaves, which should, along with other physical foliage traits, allow greater gall-forming insect survivorship in the canopy and result in higher leaf-chewing damage In the understorey. The study was conducted in the subtropical rainforest of Lamington National Park, Queensland, Australia. Along an altitudinal gradient, four independent canopy pin-transects and one equivalent, horizontal understorey pin-transect (20 metres long) were conducted at each of four altitudes, 300, 700, 900 and 1100 m above sea level (a.s.l.). Each discrete layer (stratum) of foliage within the 1 m diameter pin-transects was considered a sample. From each sample, various leaf and meristem measurements were taken, and the number of damaged leaves was counted. Healthy leaves were also collected for analysis of specific leaf mass, an indirect measure of sclerophylly. All vegetation resources were more abundant in the canopy than in the understorey, and also increased from lower to higher altitudes. In the canopy, leaf density increased steadily from 300 to 1100 m sites, but in the understorey 300 and 900 m had denser foliage than 700 and 1100 m. Young leaves were more available in the canopy than the understorey. However, the sites at 900 and 1100 m had as many young leaves in the understorey as 300 m sites had in the canopy. The ratio of young/mature leaves increased with altitude, with no difference between understorey and canopy. Leaf area did not vary between canopy and understorey. Active meristems were found in greater numbers in the canopy. A significant increase in sclerophylly with increasing canopy stratum height was found. Comparing altitudes, 300 and 1100 m sites had more active meristems than those at 700 and 900 m. Out of 72 plant species, 29 presented galls of which the greatest densities were concentrated on seven host species. Herbivory was more intense at lower altitudes, suggesting that micro-climate and host specificity may drive the insect distribution patterns ❐ *canopy-understorey vegetation gradient, gall density, leaf herbivory, gall super hosts, Lamington National Park, sclerophyllous habitats.*

Herbivorous insect species diversity and population parameters are affected by the quality and distribution of their food resources, in particular leaves. Nevertheless, little has been done to describe forest canopy traits at the scale which is relevant for herbivores: the foliage. Leaf area, spatial distribution, density and sclerophylly may be measured, along with the distribution of damaged leaves, and thus produce direct information on how leaf traits affect the distribution of herbivory. Recently Ribeiro and Basset (2007) showed the importance of sclerophylly and leaf density for gall-forming and leaf-chewing herbivory. The positive response of galls to increasing sclerophylly with canopy height and an accompanying inverse response of leaf-chewing seem to be strong ecological patterns, likely to be repeated in a variety of distinct forest types.

Gall-forming insect species are highly specialist endophagous insects. The mechanisms by which their larvae interact with leaves have been the focus of many ecological studies and of a number of important hypotheses (Price 1994; Price *et al.* 1998; Mendonça 2001). Gall insects manipulate the leaf tissues, inducing nitrogen-richer cells to grow, surrounding the larvae. As a consequence, this guild strongly contrasts with free-feeding, leaf-chewing herbivores. Gall species are specialists and adapted to low nutritional leaves, whilst leaf chewers tend to be generalist species, closely dependent on the natural nutrient content of the host leaves (Coley *et al.* 1985; Herms & Mattson 1992; Novotny & Basset 2000; Novotny *et al.* 2002). Recent studies on gall diversity in Panama have shown a substantially larger number of galls in the canopy of tropical forests than in any other ecosystem (Ribeiro & Basset 2007). These authors demonstrated that the upper canopy is a sclerophyllous and harsh environment compared to the understorey, thus favourable for gall survivorship.

Although the distribution of gall-forming species is considered to be strongly related to sclerophylly, it is also highly correlated with a limited number of host taxa that have galls in each ecosystem, or within a habitat in each ecosystem. For instance, although gall populations were larger in the canopy compared to the understorey, galls were only found on 16 plant species in San Lorenzo Park, Panama, representing only 22% of sampled tree species (Ribeiro & Basset 2007). Both Price (1977) and Fernandes (1992) proposed that gall diversity is positively related to plant family size (i.e. the number of species in families), but neither author actually discussed how the evolutionary constraints that restrict gall-forming species to so few host choices may affect the global pattern of gall species distribution.

In addition, until Ribeiro and Basset (2007) there was no methodology available to compare gall abundance or leaf herbivory in a way that compensates for differences in vegetation densities along vertical gradients in forests. A sampling protocol that explicitly accounts for vegetation density in comparable habitat volumes not only allows the adequate comparison of herbivory levels, but also enables proper quantification of the distribution of vegetation within and between sites and habitats.

The present work describes the variation in forest foliage traits, such as leaf strata (discrete layers of foliage), leaf density, active meristem density and leaf sclerophylly, between habitats and along an altitudinal gradient in a subtropical, mesic, cloud forest in south-eastern Queensland. We also examine how gall density and herbivory is distributed from the understorey to the canopy, along the same altitudinal gradient.

MATERIALS AND METHODS

Study sites and canopy access. Research was conducted in subtropical rainforest in Lamington National Park, Queensland, Australia. The park has an area of 20590 ha, and belongs to the Gondwana Rainforests of Australia World Heritage Area. It has an altitudinal gradient ranging from around 200 m to 1150 m above sea

level (a.s.l.). The rainforest of the highest elevations is simple microphyll fern forest dominated by *Nothofagus moorei* (Fagaceae). Climate is seasonal, with most of the annual rainfall (1800 mm) occurring in the summer months (between November to March). In the winter the temperature can fall as low as 0° C overnight (see Strong *et al.* 2011). Sampling was undertaken as part of the larger IBISCA-Queensland Project described in Kitching *et al.* (2011). This project provided the framework for this study and established a series of four permanent plots (A-D) at each of five altitudinal categories (300, 500, 700, 900 and 1100 m a.s.l.). Due to difficulties with site access and associated safety constraints for sampling with single rope climbing techniques, the 500 m altitude sites could not be used in this project. All other altitudes were sampled.

Samples were taken in October 2006, during the early wet season, and again in March-April 2007, in the early dry season. This was an exceptionally dry period, with rainfall ranging from 200-300 mm in the October sampling period, and from 100-200 mm in April, in both cases below the historic mean precipitation (Bureau of Meteorology, Qld Climate Service Centre: http://www.bom.gov.au/climate/).

Sampling protocol – the pin-cylinder transect. Vegetation traits and herbivory were measured, and galls sampled, on all leaves within a volumetric cylinder space of one metre in diameter, settled in both vertical and horizontal sections of the forest. For the 'canopy-pin transect', each cylinder transect started at the upper canopy and finished at three metres above the ground. For the 'understorey-pin transect', it followed an equivalent horizontal transect of 20 m (the average height of this forest) parallel to and at 10 cm above the soil surface, thus preventing sampling seedlings. This method is similar to the pin-quadrat method used in phytosociological surveys of grasslands (Borges & Brown 1999), but instead of counting leaf touches, we counted leaves and galls found inside this cylindrical volume. Within each transect, a sample was taken as a discrete layer of foliage, i.e. a continuous group of leaves separated by a distinct gap from the next group, hereafter called a leaf stratum (see details in Ribeiro & Basset 2007). Four independent canopy pin-transects (one per plot) and one horizontal understorey pin-transect were conducted per altitude (300, 700, 900 and 1100 m a.s.l.). The understorey pin-transects were set in the plots 300C, 700A, 900B, and 1100C, by random choice.

From each sample, the total number of leaves, the number of young leaves, the number of buds and active meristems and the number of damaged leaves were counted. Leaf herbivory was estimated by counting all leaves with more than 10% of the leaf area lost, estimated visually. Since this figure represents the global average leaf area loss in tropical wet forests, leaves scored above this average may be considered 'substantially damaged' (Coley & Aide 1991), and we used the proportion of damaged/total leaves per stratum as our estimate of free-feeding herbivory. Healthy leaves were collected for analysis of specific leaf mass, an indirect measure of sclerophylly. Specific mass per leaf area unit (Cooke *et al.* 1984) was obtained by dividing leaf dry weight by area, using mature leaves collected in 2006. To estimate gall densities, all leaves in a sample with galls, or any gall-like imperfection, were collected, counted and frozen for future analyses. Detailed analyses of the causes of mortality of galls will appear elsewhere.

Statistical analyses. The effects of altitude and forest habitat (understorey versus canopy) on vegetation traits and herbivory were tested in a mixed ANCOVA model, with sample sites set as random factors and altitude as a covariate, or with bifactorial models, taking altitude as fixed factors in interaction with habitat. The model choice depended on the hypothesis and the assumed necessity to explicitly incorporate the site variation in the model – first option – or to test variance between individual altitudes rather than altitude as whole – second option. In these analyses, the mean canopy pin transect

data were compared with the understorey pin transect data. Some dependent variables were ln(x+1) transformed, to satisfy the assumptions of normality. Proportion of damaged leaves was transformed by the arsine of the square root. All models were analysed using in SPSS 17.0.

RESULTS

Forest vegetation traits and herbivory distribution. All vegetation resources were more abundant in the canopy than in the understorey, and also increased from the lower to the higher altitudes (Figs 1, 2). The particulars are worthwhile exploring.

Foliage volume and young leaves. Total leaves, as expected, were much denser in the canopy than in the understorey (ANOVA, $F_{1;160} = 182.5$, $p<0.0001$, Fig. 1). Although leaf density in the canopy increased steadily from 300 m to 1100 m, in the understorey leaf density did not vary substantially between altitudes, resulting in a significant interaction between these factors (ANOVA $F_{3;160} = 3.4$, $p <0.05$, Fig. 3). Young leaves were more available in the canopy than in the understorey, but the difference was marginally significant ($p <0.07$) due to a stronger interaction between habitat and altitude: the plots at 900 and 1100 m showed as many young leaves in the understorey as in the canopy of plots at 300 m (ANOVA $F_{1;150} = 9.6$, $p <0.01$, Figs 2, 3). The understorey at 300 and 700 m had the lowest amounts of young leaves. Interestingly, the ratio of young to mature leaves increased consistently with altitude, with no difference between understorey and canopy ($y = 0.00018$; $r^2 = 0.48$, $p <0.0001$; effect of habitat – t-test = 1.6, $p = 0.113$, Fig. 3). On the other hand, leaf area did not vary between canopy and understorey, and was greater at 300 and 700 m than at other altitudes (LSD, $p <0.05$). This result reflects larger leaves in the understorey than in the canopy, but also a substantially large variation in the data (Fig. 4).

Finally, there was little variation in the number of leaf strata. The mean number of strata for all transects was 5.4, and the 900 m altitude had the greatest number (mean = 7.25) and the only forest with eight strata (in three of the four transects). The minimum number of strata was three, found at 300 m and 1100 m.

Buds and meristems. Active meristems, namely young vegetative and reproductive buds, flowers and fruits, comprise a very particular type of resource for herbivorous insects. Unequivocally, most of these resources were found in greater numbers in the canopy (ANOVA, $F_{1;160} = 141.3$, $p < 0.0001$, Fig. 4). Comparing altitudes, the 300 and 1100 m plots had more active meristems than those at 700 and 900 m sites (ANOVA, $F_{3;160} = 4.4$, $p < 0.04$, Fig. 4).

A strong positive correlation between leaf sample height in the canopy and sclerophylly was found ($y = 0.0075 + 0.00020$ [Median height]; $r^2 = 0.41$; $F_{1,161} = 112.3$, $p < 0.0001$ Fig. 5), consistent across all altitudes. Leaf area lost by chewing (estimated only for 2006) showed a significant negative response to canopy height, although there was no direct response to sclerophylly. However, the regression model explained low levels of the data variance ($y = 0.36 - 0.0052$ [median height]; $r^2 = 0.04$; $F_{2,160} = 3.3$, $p < 0.05$), even though leaf chewing was still significantly greater in the understorey than in the canopy (t-test $_{172} = 1.97$, $p < 0.001$). Regardless of a greater availability of vegetation resources at the 1100 m plots, herbivory was more intense at the lower elevation plots ($F_{3,154} = 4.48$, $p < 0.005$).

Gall distribution among tree species. In 2006, we sampled 59 tree and shrub species (Appendix 1), of which 25 species (42%) had galls. Also, 35% of individual sampled plants had galls, reflecting a great concentration of galls in few hosts. A total of 4089 galls were sampled in this year, from 61 107 sampled leaves. Interestingly, 80% of these galls were concentrated on six host species (*Argyrodendron actinophyllum*, *Argyrodendron trifoliolatum*, *Arytera divaricata*,

FIG. 1. Comparison of the total numbers of leaves, young leaves and other resources (buds + active meristems) sampled in the understorey and the canopy, summed across four elevations (300, 700, 900 and 1100 m a.s.l.) in Lamington National Park IBISCA-Qld plots. Understorey values are based on the sum of data from four pin-transects (one per plot). Canopy values are based on the sum of data from 12 pin transects (four per plot) divided by four.

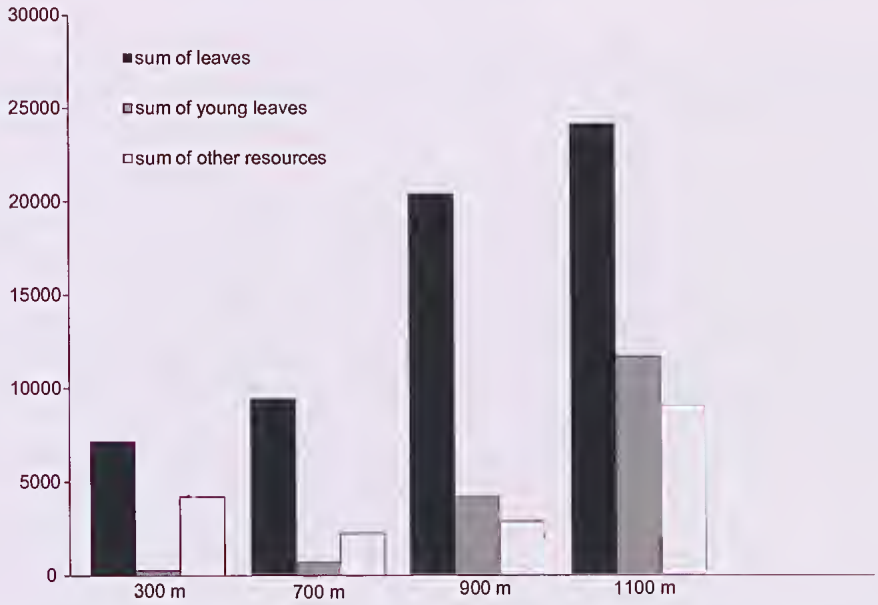


FIG. 2. Total numbers of leaves, young leaves and other resources (buds + active meristems) sampled from four different altitudes (300, 700, 900 and 1100 m a.s.l.) in rainforest at Lamington National Park. Each bar based on data from four canopy pin transects and one understorey pin transect.

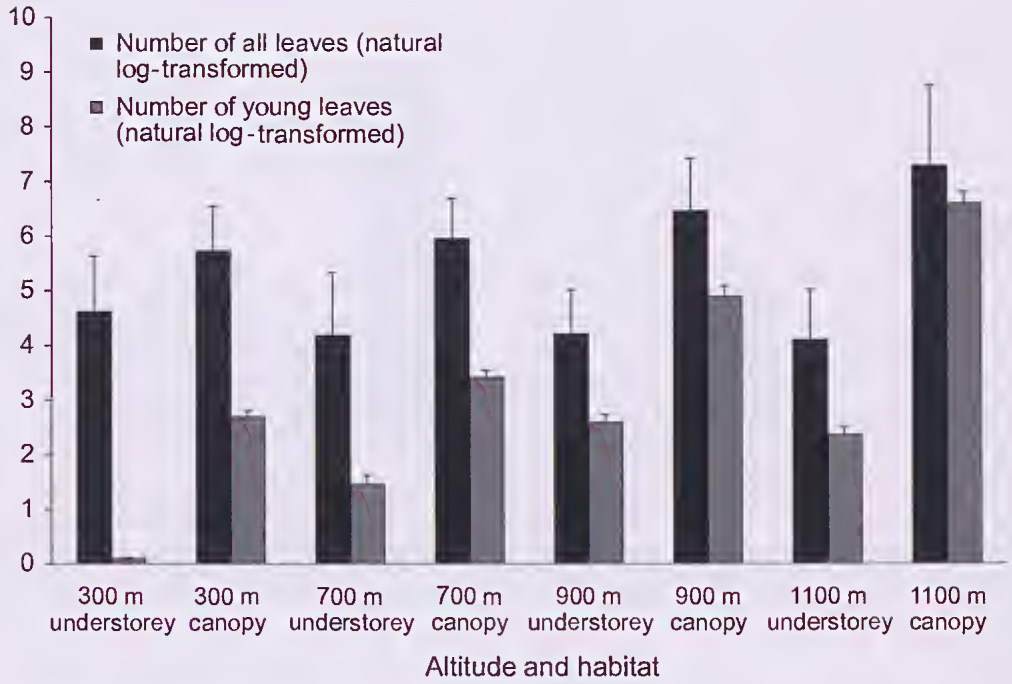


FIG. 3. Foliage traits, mean number of leaves (solid bars) and mean number of young leaves (shaded bars), both ln(x+1) transformed, in the understorey and canopy of rainforest within each of four altitudes (m a.s.l.) at Lamington National Park, Queensland.

Caldcluvia paniculosa, Melodinus australis, Orites excelsa).

In 2007, only 49 tree and shrub species were sampled, but 18% of these were new species not sampled in the 2006 survey, thus a total of 72 species were sampled (out of 329 plant individuals - 164 in 2006 and 165 in 2007), from which 40% (29 species) had some gall tumours. A total of 10 805 galls were sampled in 2007 from 26 854 sampled leaves. However, 65% of these were collected from only three individual branches of a single *Ficus watkinsiana* tree (an average of 16.6 galls per leaf). Of the remaining galls, 18% were from *Argyrodendron trifolialatum* and 10% from *Arytera divaricata*. Other galled plant species were the same as those from the 2006 collection. In summary, only seven species, or 9.7% of the total number of identified plants (and 24% of galled plant species), accumulated the majority of sampled galls.

Exceptionally, a high understorey gall density was observed at 300 m, caused by a specific infestation of three young individuals of the tree *Arytera divaricata*. However, 19% of the sampled galls on these hosts were dead. The much greater leaf density found in the wetter season in October 2006 seemed to substantially affect the gall density pattern, as most of the galled tree species were found in this year, compared to a much more concentrated density of galls on only one species, *Ficus watkinsiana*, in autumn 2007.

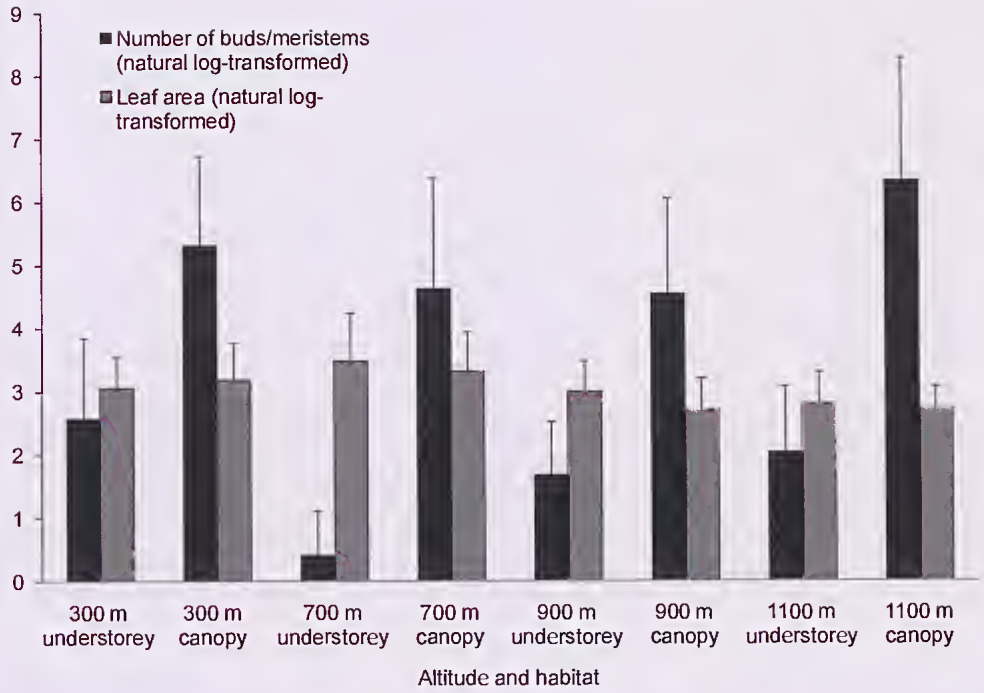


FIG. 4. Meristematic resources, mean number of buds and meristems (solid bars) and mean leaf area (shaded bars), both ln(x+1) transformed, in the understorey and canopy of rainforest within each of four altitudes at Lamington National Park, Queensland.

DISCUSSION

The *Nothofagus* forest at 1100 m showed a remarkably distinct amount of plant resources compared with all other altitudes. The larger amounts of resources available in these high altitude forests included leaves, young leaves and active meristems. Moreover, the average leaf sclerophylly for the understorey was lower at 1100 m compared to that at 900 m (LSD, $p < 0.03$). Nevertheless, the 1100 m plots showed the smallest proportion of chewed leaves. While gall insects responded closely to the presence of specific host species or sclerophyllous habitat (see below), free-feeding herbivores did not respond so directly to the general availability of vegetation resources. Conversely, the observed pattern of higher leaf chewing herbivory at 300 m may reflect some level of specificity, either in host species or in micro-climate. In addition, the 300 m plots had the second highest availability of vegetation resources in comparison with other elevations, and the substantial leaf damage observed at this altitude may be due to an optimum combination of climate and resources, thus resulting in high levels of insect herbivory. Additional IBISCA-Queensland data on the distribution and abundance of insect species may help elucidate the influence of vegetation traits on forest biodiversity.

. A clear pattern of highly concentrated gall densities on few host species and few host individuals, along with an outbreak phenomenon in early autumn, defined the gall-former insect distribution at the study sites. In addition,

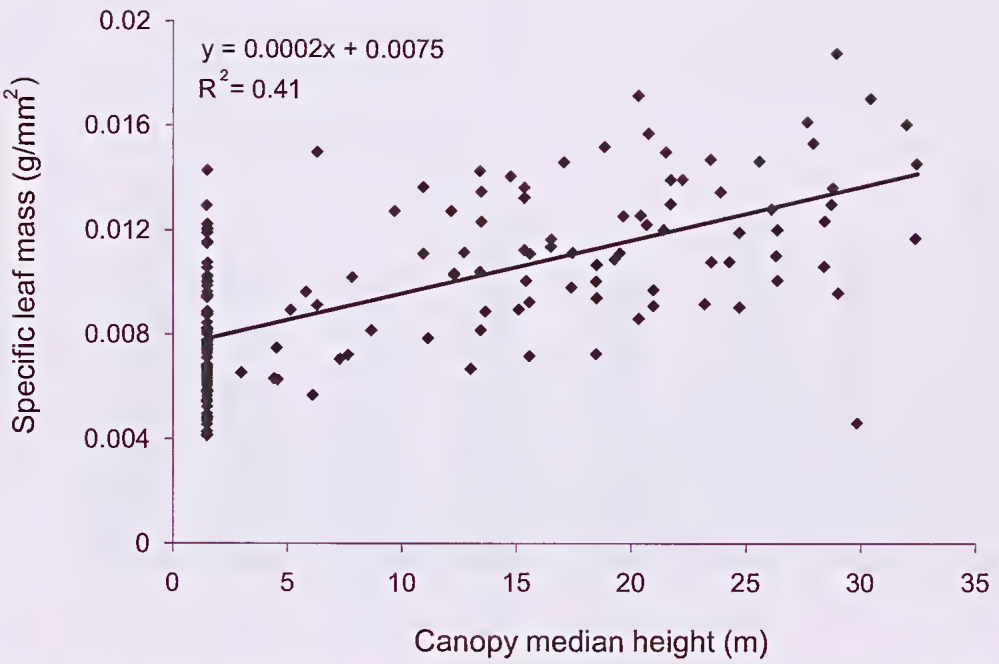


FIG. 5. Relationships between leaf sclerophylly (specific leaf mass) and sample height above the ground (canopy median height), based on multiple plant species sampled across four altitudes (300, 700, 900 and 1100 m a.s.l.) in Lamington National Park, Queensland.

the expected predominance of galls in the canopy compared to the understorey was observed in the 2006 spring sample, regardless of altitude. However, this pattern disappeared in 2007 due to a highly patchy distribution of galls on few trees, and the total absence of live galls in any understorey plant above 300 m (unpub. data). The much greater leaf density found in the wetter season in 2006 seemed to substantially affect the gall density pattern, as most of the galled tree species were found in this season, compared with a much more concentrated density of galls on only one species, *Ficus watkinsiana*, in the following early dry season. Therefore, the present work has shown an important non-synchronised pattern in gall distribution, clearly contrary to Mendonça's (2001) prediction, but providing strong support for the relative importance of the super host hypothesis (Price 1994; Mendonça 2007). As predicted by Fernandes (1992), the most frequently attacked and densely infested host species belonged to large pantropical families, such as Sterculiaceae (*Argyrodendron*), Moraceae (*Ficus*), Sapindaceae, Apocynaceae and Proteaceae, all with more than 60 genera, and some (Moraceae) with more than 1000 species. *Caldcluvia paniculata* was the only exception, belonging to the Cunoniaceae, a family with 25 genera. Another galled species of note is *Orites excelsa* (Proteaceae). This species has a fossil record from the early Cenozoic, and is found in all southern continents, probably because of a Gondwanan distribution (Larew 1986; Tahvanainen & Niemela 1987). Hence, we have evidence of galls successfully infesting both large and old plant families, a pattern only partially supported by Fernandes' (1992) data.

The Lamington rainforest showed a very strong and clear pattern of increasing

TABLE 1. Identified plant species sampled from canopy and understorey pin transects along an altitudinal gradient at Lamington National Park, Queensland and their occurrence at IBISCA-Queensland study plots (see Kitching *et al.* 2011 for plot details). * indicates those species with galls.

Plant species	Plant family	IBISCA-Qld altitude/plots
Acmena ingens	Myrtaceae	700A
Acmena smithii	Myrtaceae	900B
Acradenia euodiiformis *	Rutaceae	900C
Acronychia pubescens	Rutaceae	900D
Anthocarapa nitidula *	Meliaceae	900A; 700A
Aphananthe philippinensis	Ulmaceae	300B
Argyrodendron actinophyllum subsp. *actinophyllum**	Euphorbiaceae	300C; 700D; 900A
Argyrodendron trifoliolatum *	Euphorbiaceae	700A, B
Arytera distylis	Sapindaceae	300D
Arytera divaricata *	Sapindaceae	300C, D; 700A
Atalaya multiflora	Sapindaceae	300C
Atractocarpus benthamianus	Rubiaceae	1100C
Austrosteenisia glabristyla	Fabaceae	700B; 900C, D; 1100A
Baloghia inophylla *	Euphorbiaceae	700A, B, D; 900A
Brachychiton discolor	Malvaceae	300D
Caldcluvia paniculosa *	Cunoniaceae	900C; 1100A,C
Castanospermum australe	Fabaceae	300A
Cephalaralia cephalobotrys	Araliaceae	1100C
Cissus antartica *	Vitaceae	300B
Cissus sterculiifolia	Vitaceae	900B
Citronella moorei	Leptaulaceae	300A
Cleistanthus cunninghamii	Phyllanthaceae	300A, C; 700A
Cryptocarya obovata	Lauraceae	900B
Daphnandra apatela	Atherospermataceae	700A
Denhamia celastroides	Celastraceae	900B
Diospyros pentamera	Ebenaceae	700A, B; 900C
Diploglottis australis	Sapindaceae	700A
Doryphora sassafras	Atherospermataceae	1100C
Drypetes deplanchei	Putranjivaceae	700C; 1100C
Elattostachys nervosa *	Sapindaceae	700A

TABLE 1. cont...

Plant species	Plant family	IBISCA-Qld altitude/plots
Endiandra muelleri subsp. *muelleri**	Lauraceae	700A; 900D
Ficus macrophylla forma *macrophylla*	Moraceae	300C
Ficus watkinsiana *	Moraceae	300B; 900D
Flindersia australis *	Rutaceae	300 D
Gossia acmenoides *	Myrtaceae	300 C
Halfordia kendack *	Rutaceae	900B
Harpullia hillii	Sapindaceae	700A
Helicia gabriflora	Proteaceae	900A, B
Hodgkinsonia ovatiflora	Rubiaceae	300D
Litsea reticulata	Lauraceae	900 C
Lophostemon confertus *	Myrtaceae	300A; 700D
Melodinus australis *	Apocynaceae	700A; 900B, C, D; 1100A, C
Melodorum leichhardtii *	Annonaceae	300B,D
Myrsine subsessilis subsp. *subsessilis*	Myrsinaceae	1100C
Neolitsea australiensis	Lauraceae	700A; 900B
Nothofagus moorei	Notofagaceae	1100C, D
Orites excelsa *	Proteaceae	900B; 1100A, B, C
Pararistolochia laheyana	Aristolochiaceae	1100C
Planchonella australis	Sapotaceae	300C
Polyosma cunninghamii	Escallionaceae	900B; 1100D
Polyscias elegans	Araliaceae	700A
Pseudoweinmannia lachnocarpa *	Cunoniaceae	300B; 700C
Psychotria simmondsiana var. *simmondsiana*	Rubiaceae	1100C
Psydrax odorata	Rubiaceae	300C
Quintinia sieberi *	Quintiniaceae	1100B, C
Quintinia verdonii	Quintiniaceae	900B
Ripogonum album	Ripogonaceae	900B
Ripogonum discolor	Ripogonaceae	1100C
Ripogonum fawcettianum	Ripogonaceae	900D; 1100C
Sarcopteryx stipata	Sapindaceae	900B
Stenocarpus salignus *	Proteaceae	900B

TABLE 1. cont...

Plant species	Plant family	IBISCA-Qld altitude/plots
Streblus brunonianus	Moraceae	700A
Syzygium oleosum	Myrtaceae	1100C
Tasmannia insipida	Winteraceae	300C
Tetrastigma nitens *	Vitaceae	300B, C, D
Triunia youngiana *	Proteaceae	900B; 1100C
Trophis scandens subsp. *scandens* *	Moraceae	300B
Vitex lignum-vitae	Lamiaceae	300C
Wilkiea austroqueenslandica	Monimiaceae	900B
Wilkiea huegeliana	Monimiaceae	900B

sclerophylly with canopy height, in accordance with our predictions. Nevertheless, the effects of sclerophylly and sample median height were not significantly collinear when tested against gall density (unpub. data). As the galls are strictly related to their host plants, they track the host even though there might be more and different sclerophyllous leaves available in the ecosystem. Although micro-habitat harshness and sclerophylly have been shown to determine gall insects' oviposition preferences and/or survivorship (Fernandes & Price 1988, 1992; Ribeiro & Basset 2007), in Lamington National Park these mechanisms were partially masked by the idiosyncrasies of the very few super host species present in the area.

Finally, although most leaf chewing tended to occur in the understorey, a substantially high variation in the data may have resulted in lack of a direct relationship with sclerophylly. In addition to this scattered distribution of leaf chewing, we also observed that gall distribution did not predominate exclusively in the canopy, as predicted. Namely, the gall distribution pattern was affected by host specificity in the early dry season. Canopy sclerophylly was considered the mechanism behind both increasing gall density and decreasing leaf chewing herbivory (Ribeiro & Basset, 2007). However, one specific aspect about the Lamington forest must be emphasised. While wet tropical forests, such as that found in Panama, had leaf sclerophylly mostly varying from 0.0014 to 0.01 g/mm^2 in the understorey, at Lamington understorey sclerophylly consistently ranged from 0.004 to 0.0140 g/mm^2. Therefore, a relatively more sclerophyllous vegetation at ground level in Lamington may mask the predicted ecological response, namely an inverse distribution pattern in the leaf chewing and leaf galling herbivore guilds, which should be related to soft-hard leaf variation.

In conclusion, it seems necessary to generate a world-wide range of complementary studies covering overlooked ecosystems and habitats in terms of vegetation and herbivory parameters. The IBISCA research model (see Kitching *et al.* 2011) has enabled the opportunity to conduct insect studies across the globe in order to clarify questions such as those examined, related to insect species density and diversity in forest habitats.

ACKNOWLEDGEMENTS

A project such as IBISCA-Queensland cannot function without major funding. We are deeply grateful to the Department of State Development of the State of Queensland for the Smart State

funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Global Canopy Programme, NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. We also received cash support from the federal Department of Environment, Heritage and the Arts and O'Reillys' Rainforest Resort. We are grateful to all these sources without which the project would not have been possible. O'Reilly's Rainforest Resort and the Mt Cainbable Cabins provided accommodation and sustenance. We thank Sarah Boulter for reviewing the text and helping with fieldwork, and Stefan Curtis, Jankees van der Have, Sarah Maunsell, Daniel Pamin and Kalsum Mohd Yusah for their contributions to the fieldwork. Global Canopy Programme and the Foreign and Common Wealth Office of the British Embassy in Brazil provided MB with climbing gear; Universidade Federal de Ouro Preto and the Post-Graduate Programme in Ecology of Tropical Biomes provided MB with training in climbing techniques. SPR is supported by grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq.

LITERATURE CITED

Basset, Y. 1991. The spatial distribution of herbivory, mines and galls within an Australian rain forest tree. *Biotropica* **32**: 271-281.

Borges, P.A.V. & Brown, V.K. 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society* 66: 373-410.

Coley, P.D. & Aide, T.M. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forest. Pp. 25-49. *In*, Price, P.W., Lewinsohn, T.M., Fernandes G.W. & Benson, W.W. (eds.) *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (Wiley: New York).

Coley, P.D., Bryant, J.P. & Chapin, F.S.III 1985. Resource availability and plant antiherbivore defense. *Science* **230**: 890-899.

Cooke, F.P., Brown, J.P. & Mole, S. 1984. Herbivory, foliar enzyme inhibitors, nitrogen and leaf structure of young and mature leaves in a tropical forest. *Biotropica* **16**: 257-263.

Espírito-Santo, M. & Fernandes, G.W. 2007. How many species of gall-inducing insects are there on earth, and where are they? *Annals of the Entomological Society of America* **100**: 95-99.

Fernandes, G.W. & Price, P.W. 1988. Biogeographical gradients in galling species richness: tests of hypotheses. *Oecologia* 76: 161-167.

Fernandes, G.W. & Price, P.W. 1992. The adaptative significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia* 90: 14-20.

Fernandes, G.W. 1992. Plant family size and age effects on insular gall-forming species richness. *Global Ecology and Biogeography Letters* 2: 71-74.

Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review in Biology* 67: 283-335.

Larew, H.G. 1986. The fossil gall record: a brief summary. *Proceedings of the Entomological Society Washington* **88**: 385–388.

Lowman, M.D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* **10**: 7-24.

Medianero, E. & Barrios, H. 2001. Riqueza de insectos cecidógenos en el dosel y sotobosque de dos zonas ecológicas en Panamá. *Scientia* 16: 17-42.

Medianero, E., Valderrama, A. & Barrios, H. 2003. Diversidad de insectos minadores de hojas y formadores de agallas en el dosel y sotobosque del bosque tropical. *Acta Zoologica Mexicana* 89: 153-168.

Mendonça, M.S. Jr. 2001. Gall insects diversity patterns: the resource synchronisation hypothesis. *Oikos* 95: 171-176.

Novotny, V. & Basset, Y. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89: 564-572.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek L. & Drozd. P. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**: 841-844.

Price, P.W., Fernandes, G.W., Lara, A.C.F., Brawn, J., Barrios, H., Wright, M., Ribeiro, S.P. & Rothcliff, N. 1998. Global patterns in local number of insect galling species. *Journal of Biogeography* 25: 581-591.

Price, P.W. 1994. Phylogenetic constraints, adaptative syndromes, and emergent properties: from individuals to population dynamics. *Research in Population Ecology* 36: 3-14.

Price, P.W. 1977. General concepts on the evolutionary biology of parasites. *Evolution* 31: 405-420.

Ribeiro, S.P. 2003. Insect herbivores in the canopies of savannas and rainforests. Pp. 348-359. *In*, Basset, Y., Novotny, V., Miller, S. & Kitching, R. (eds.). *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy* (Cambridge Press: New York).

Ribeiro, S.P. & Basset, Y. 2007. Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: the importance of leaf sclerophylly. *Ecography* 30: 663-672.

Tahvanainen, J. & Niemela, P. 1987. Biogeographical and evolutionary aspects of insect herbivory. *Annals Zoologica Fennici* 24: 239-247.

Veldtman, R. & McGeoch, M.A. 2003. Gall-forming species richness along a non-scleromorphic vegetation rainfall gradient in South Africa: the importance of plant community composition. *Austral Ecology* 28: 1-13.

Memoirs of the Queensland Museum | **Nature**

55 (1-2)

PUBLISHED BY ORDER OF THE BOARD

Memoirs of the Queensland Museum | Nature • 2010 - 2011 • 55

Memoirs of the Queensland Museum | **Nature**

Volume 55 is complete in two parts

PO Box 3300, South Brisbane 4101 Qld, Australia
Phone 61 3840 7555
Fax 61 7 3846 1226
www.qm.qld.gov.au

National Library of Australia card number
ISSN 0079-8835

A Guide to Authors is displayed at the Queensland Museum web site www.qm.qld.gov.au/organisation/publications/memoirs/guidetoauthors.pdf

A Queensland Government Project
Typeset at the Queensland Museum

TABLE OF CONTENTS

Part 1 (issued 15 March 2010)

Part 2 (issued 20 December 2011)

CONTENTS CONTINUED

CONTENTS