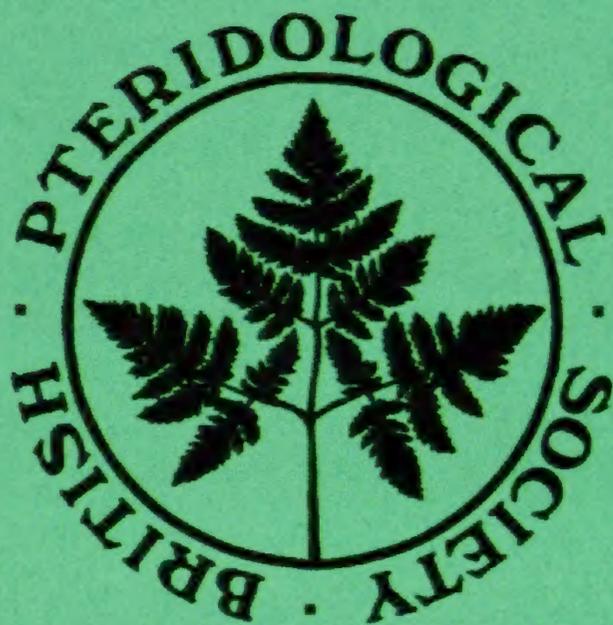


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**THE  
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**Editors:**

**M. GIBBY & A. LEONARD**

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**WHAT IS THE MINIMUM AREA NEEDED TO ESTIMATE THE BIODIVERSITY OF PTERIDOPHYTES IN NATURAL AND MAN-MADE LOWLAND FORESTS IN MALAYSIA AND SINGAPORE?**

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Key words: pteridophytes, species-area curve, natural forest, man-made forest, Malaysia, Singapore

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**ABSTRACT**

The present studies show that in man-made forests, six 10 m x 10 m quadrats are sufficient to give a good representation of the species diversity, as the comparatively uniform environment can provide a suitable habitat for only a limited number of species. Contrastingly, nine 10 m x 10 m quadrats are still not sufficient to capture the characteristic diversity of pteridophytes in natural forest habitats. This is due to the highly scattered distribution patterns of forest herbs, including the pteridophytes, along different gradients and microhabitats in the forest. In order to estimate the diversity of pteridophytes in natural forests more accurately, a minimal sample size of more than nine 10 m x 10 m quadrats needs to be established.

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**INTRODUCTION**

Systematic collection and documentation of the diversity of pteridophytes in Singapore started as early as the 19<sup>th</sup> Century (Turner, 1994), and in Peninsular Malaysia in the early part of the 20<sup>th</sup> Century (Bidin, 1991). However, most of these studies concentrated on the taxonomy and species listings of pteridophytes. To date, few studies in tropical Southeast Asia have used quantitative methods to estimate the diversity of pteridophytes in a given area. Johnson (1969) appears to have been the first to conduct a quadrat survey of non-tree forest species (including pteridophytes) in this region. Her 15 quadrats in Taman Negara, Peninsular Malaysia, each of one square chain (about 0.6 km<sup>2</sup>), yielded a low number of 7 species of ferns and fern allies. A notable recent study by Sato *et al.*, (2000) employed cubic quadrats of various sizes and numbers in an attempt to characterize the diversity of the pteridophyte flora in an oil palm plantation and three natural forests (Kepong, Pasoh and Semangkok) in Malaysia. Expectedly, the results showed that the number of quadrat cubes needed to capture the maximum pteridophyte diversity depends on the quadrat cube size used and the locally existing biodiversity. For the natural forest at Semangkok, 20 quadrat cubes of 20 m x 20 m x 20 m were needed to capture the high number of 40 species of ferns, whereas in the natural lowland forest at Kepong, the 20 quadrat cubes of 20 m x 20 m x 20 m captured a maximum number of about 28 species. In the oil palm plantation, 14 quadrat cubes of 20 m x 20 m x 20 m were needed to capture the maximum number of 18 species.

Since the objective of sampling, as opposed to documenting each and every species or individual, is to reduce the amount of labour and time involved (Chapman, 1976), the present study aimed to find out the minimum number of quadrats with a manageable area size of 10 m x 10 m that would be needed to estimate the pteridophyte diversity of natural lowland rain forest and man-made forests (oil palm and rubber plantations) in both Johor (Peninsular Malaysia) and Singapore.

### STUDY SITES AND METHODS

Five sampling sites in natural and man-made forests in Johor (Peninsular Malaysia) and Singapore were selected for the present investigation. The two natural forests selected were the Gunung Pulai Forest Reserve [GPFR], situated inside the Gunung Pulai Recreation Forest (1° 36'N, 103° 34'E) in Johor, and the Bukit Timah Nature Reserve [BTNR] (103° 47'E, 1° 21'N) in Singapore. The man-made forests investigated were the oil palm and rubber plantations in the vicinity of Gunung Pulai Forest Reserve in Johor, and the rubber plantations on Pulau Ubin (1° 24' N, 103° 58' E), an island off mainland Singapore. These surveyed areas were chosen for their geographical proximity to each other, so as to eliminate the effect of climatic factors as a possible cause for the difference in the species diversity observed.

Initially, six non-contiguous quadrats of 10 m x 10 m were established in each of the five study sites. The measurement of 10 m x 10 m was selected in consideration of the morphology and distribution pattern of the plant group to be sampled. According to Causton (1988), a quadrat size of up to 0.25 km<sup>2</sup> is suitable for the sampling of herbaceous vegetation. Since pteridophytes are comparatively not large herbaceous plants (with some exception, like *Cyathea* sp.), and after conducting a preliminary survey at the selected study sites, a quadrat size of 10 m x 10 m was deemed suitable for this study.

In placing the quadrats, a ground survey of Gunung Pulai Recreation Forest was carried out and six seemingly undisturbed forested sites were selectively identified, each located within a reasonably homogenous topography. The non-random selective method was adopted where the quadrats were preferentially located by sight to ensure that at least one individual pteridophyte was present in each quadrat. This pre-determined layout of quadrats in the natural forests was aimed to maximize the capturing of diversity of pteridophytes using the minimal number of quadrats.

In BTNR, the 2 ha permanent plot managed by the Smithsonian Institution and the National Institute of Education (NIE) was chosen to establish the six non-contiguous quadrats. Within the Smithsonian-NIE plot, the quadrat placement was similarly pre-selected in favour of the better portion of forest cover.

In the case of the two types of man-made forests in Johor and Singapore, the location of the six non-contiguous quadrats in each of the three rather homogeneous study sites was also preferentially selected to maximize the inclusion of fern diversity within the quadrat. In actual observation, the non-random selection of quadrat site was found to be not necessary in the two types of man-made forests, the rubber and oil palm plantations, because of the similarity of pteridophytic flora found *in situ*.

In all quadrats, the pteridophyte species within hand reach were recorded. Epiphytes of the high forest canopy that could not be collected from standing on the ground were excluded because the specimens could not be identified with certainty to the species even with field binoculars. The inclusion of epiphytic pteridophytes within the height of arm length in each quadrat is equivalent to, but not exactly comparable

with, the quadrat cube method used by Sato *et al.*, (2000). The microhabitat conditions for each of the pteridophytic species collected were also recorded. To complete the diversity survey, additional collections were made from the general vicinity outside the six quadrats of each study site. After the quadrat samplings, voucher materials from each study site were prepared and identified in the Cryptogam Laboratory at the National University of Singapore and verified by comparison with authentic specimens preserved at SINU and SING herbaria.

Finally, to estimate the minimum number of quadrats needed to characterize the pteridophyte species diversity in the different forest types, a species-area curve was generated for each of the five study sites.

## RESULTS

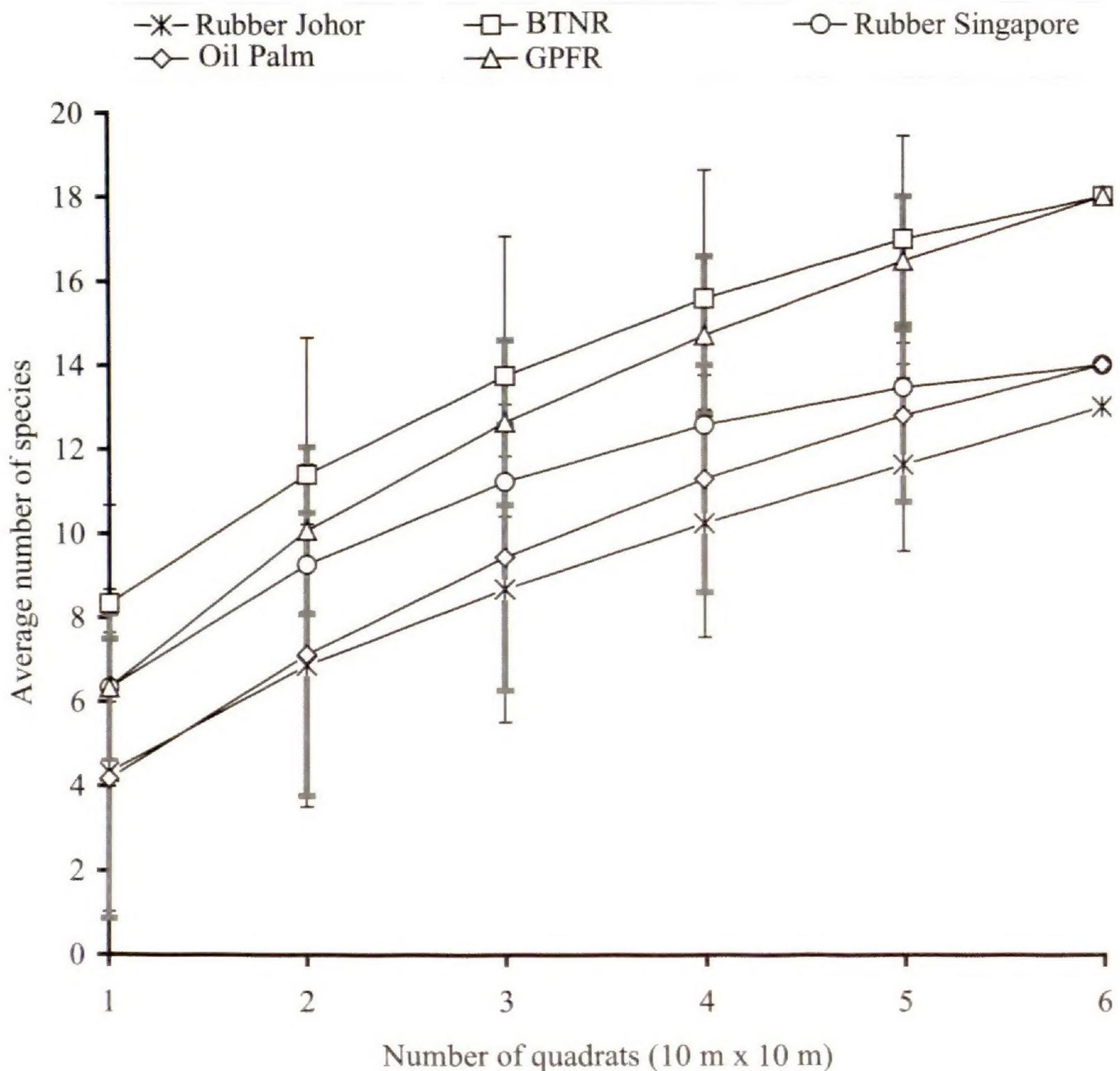
The inventory of pteridophytes present in the six quadrats in each of the five study sites yielded 18 species in GPFR, 14 species in BTNR, 18 species in the oil palm plantations in the vicinity of GPFR, 13 species in the rubber plantations in the vicinity of GPFR, and 14 species in the rubber plantations in Pulau Ubin (Table 1).

**TABLE 1.** Number of species, genera and families reported from the five study sites based on quadrat sampling.

Habitat	Natural Forests		Man-made Forests		
Locality	GPFR, Johor	BTNR, Singapore	Oil palm plantation, Johor	Rubber plantation, Johor	Rubber plantation, Singapore
Species	18	14	18	13	14
Genera	16	12	17	13	12
Families	12	10	13	11	9

Interestingly, additional collections made from the general vicinity outside the quadrats in all man-made forests showed only a small increase in the number of species in comparison with the number of species found inside the quadrats. In the oil palm plantation, only two additional species (*Selaginella willdenowii* and *Selaginella selangorensis* var. *ciliata*) were added. Similarly, in the rubber plantations in Johor and Pulau Ubin, only one species each (*Lindsaea ensifolia* and *Pteris semipinnata* respectively) was not captured by the six quadrats. Contrastingly, while the number of species found in the six quadrats was 14 at BTNR and 18 at the GPFR (Table 1), the total number of pteridophytes reported for BTNR (Wee, 1995) and the collections made from the general vicinity of established quadrats in GPFR during this study produced a high total of 95 species for BTNR and 38 species for GPFR. The listing of species of ferns and fern allies collected from the quadrats of the two types of forests investigated is given in Appendix 1.

Overall, the species-area curves generated for the five study sites (Figure. 1) showed an increase in the average number of pteridophyte species with the increase of the number of quadrats. However, the species-area curve for the oil palm and rubber plantations appeared to reach a plateau in its species number at the 6th quadrat. In contrast, the species-area curve for GPFR and BTNR continued to show an increase in species number up to the 6<sup>th</sup> quadrat. The latter trend was observed with the addition of three more quadrats of the same size to the two forest sites (Figure. 2).

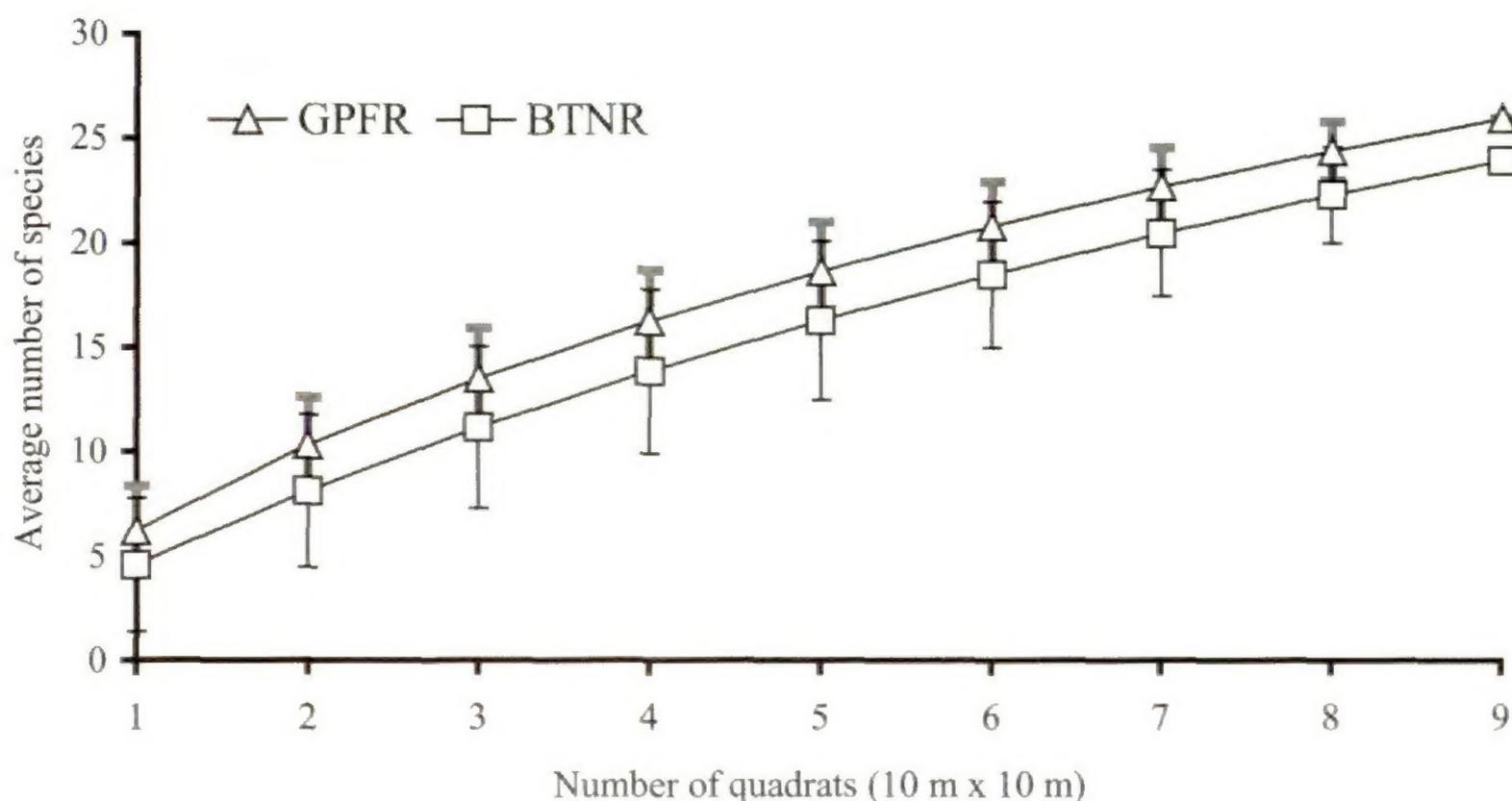


**Figure 1.** Changes in accumulating number of pteridophyte species with increase in sample size (6 quadrats) in natural and man-made forests in Peninsular Malaysia and Singapore.

### DISCUSSION

Results from this study show that a minimum of six quadrats of 10 m x 10 m is sufficient to capture the characteristic pteridophyte diversity in oil palm and rubber plantations in Johor and Singapore. This observation was confirmed when general collections made from outside the quadrats produced only two additional species in the oil palm plantation and one additional species each from the rubber plantations in Johor and Pulau Ubin.

In man-made agroforests, like the oil palm and rubber plantations, it is not surprising that a small number of six quadrats is sufficient to capture the diversity of pteridophytes. Often, agricultural landscape is associated with homogeneity of the vegetation that consists frequently of monoculture with high habitat uniformity that lacks variation in its micro-habitats. This uniformity allows a limited suite of species to colonize and survive in a rather even and predictable distribution pattern. Furthermore, in the case of the man-made forests in Johor, the regular maintenance of the plantations in the form of weeding out the non-crop vegetation also attributes to the low diversity of the pteridophytic flora.



**Figure 2.** Changes in the accumulating number of pteridophyte species with increase in sample size (9 quadrats) in the natural lowland forest in GPFR and BTNR.

The scenario appears to be different in natural lowland forests. In the case of lowland Dipterocarp forests at GPFR and BTNR, additional collections in the vicinity outside the six quadrats resulted in a notable increase in the number of species. Based on the general collections made in GPFR, the six quadrats captured only 32% of the known diversity of pteridophytes at GPFR. Likewise, only 13% of the BTNR pteridophytes reported by Wee (1995) were captured by the six quadrats. The addition of three more quadrats in GPFR and BTNR only increased the percentage of captured species diversity to 46% (26 species) in GPFR, and 22% (24 species) in BTNR. This indicates clearly that even nine quadrats of 10 m x 10 m are still far from adequate in giving a good estimation of the total pteridophytic diversity of the lowland rainforests in GPFR and BTNR.

The big differences seen in the percentage of pteridophyte diversity captured by the same number of quadrats in the two natural forests (GPFR: 32% and 46%, BTNR: 13% and 22%) are partly due to the fact that the forested area surveyed in BTNR is ca 164 ha, while the forested area surveyed in GPFR during the present study is the 8 ha of core forest around the station office. In addition, the pteridophyte flora of BTNR has been explored, studied and documented for decades by the resident staff at the Singapore Botanic Gardens since the time of British rule, resulting in the large number of species recorded from this nature reserve. In the case of the latter, the present study is a first attempt to document the pteridophyte flora of the pristine forest reserve at GPFR in Peninsular Malaysia.

The inadequacy of nine quadrats to estimate the total pteridophyte diversity of GPFR and BTNR can further be attributed to the patchy, widely spaced, and sporadic distribution pattern of pteridophytes in many lowland rain forests, making it difficult to capture the maximum representative diversity using a small quadrat size or a small number of quadrats. Understandably, the widely scattered pattern of distribution of pteridophyte species in the region is also a reflection of the heterogeneity of lowland rainforest. Similar patchy distribution in tropical rainforests is also observed in other ground vascular herbs (Kiew, 1978; Poulsen, 1996; Lum, 1999).

### CONCLUSION

For adequate estimation of the pteridophyte diversity in a man-made forest, such as the oil palm and rubber plantations in southern Malaysia and Singapore, a minimum number of six quadrats of 10 m x 10 m is sufficient. However, a total of nine quadrats of 10 m x 10 m is still insufficient to capture the overall pteridophyte diversity in the natural lowland forest in Johor (Malaysia) and Singapore. A minimum of more than nine quadrats of 10 m x 10 m is suggested for any similar studies in natural forests in the future.

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**Appendix 1.** Distribution of pteridophyte species in natural and man-made forests in Johor (Peninsular Malaysia) and Singapore based on quadrat sampling (9 quadrats in natural forest and 6 quadrats in man-made forest).

FAMILY	GENERA AND SPECIES	QUADRATS					
		NATURAL FOREST			MAN-MADE FOREST		
		GPER	BTNR	OP	RP	RU	RU
Adiantaceae	<i>Adiantum latifolium</i> Lam.	-	+	+	-	-	-
	<i>Pityrogramma calomelanos</i> (L.) Link	-	-	+	+	-	-
	<i>Syngamma alismifolia</i> (C. Presl) J. Sm.	+	-	-	-	-	-
	<i>Taenitis blechnoides</i> (Willd.) Sw.	+	+	+	+	+	+
Aspleniaceae	<i>Asplenium longissimum</i> Bl.	-	-	+	-	-	+
	<i>Asplenium nidus</i> L.	+	+	-	-	-	+
	<i>Asplenium tenerum</i> G. Forst. var. <i>retusum</i> C. Chr.	+	-	-	-	-	-
	<i>Asplenium</i> sp. 1	-	-	-	+	-	-
Blechnaceae	<i>Blechnum cf. orientale</i> L.	-	-	-	+	-	+
	<i>Blechnum finlaysonianum</i> Hook. & Grev.	+	+	-	-	-	-
	<i>Stenochlaena palustris</i> (Burm. f.) Bedd.	-	+	+	+	+	+
Cyatheaceae	<i>Cyathea contaminans</i> (Hk.) Copel.	-	+	-	-	-	-
	<i>Cyathea squamulata</i> (Bl.) Copel.	+	+	-	-	-	-
Davalliaceae	<i>Davallia denticulata</i> (Burm. f.) Mett.	-	-	+	+	+	+
	<i>Scyphularia triphylla</i> (Hook.) Fée	+	-	-	-	-	-
Dennstaedtiaceae	<i>Lindsaea divergens</i> Hook. & Grev.	+	-	-	-	-	-
	<i>Lindsaea ensifolia</i> Sw.	-	+	+	-	-	-
	<i>Microlepia speluncae</i> (L.) T. Moore	-	+	+	+	+	-

FAMILY	GENERA AND SPECIES	QUADRATS						
		NATURAL FOREST			MAN-MADE FOREST			
		GPFR	BTNR	OP	RP	RU		
Dryopteridaceae	<i>Pleocnemia irregularis</i> (C. Presl) Holtt.	-	+	+	-	-	-	-
	<i>Tectaria barberi</i> (Hook.) Copel.	+	+	-	-	-	-	-
	<i>Tectaria singaporeana</i> (Wall. ex Hook. & Grev.) Copel.	+	+	-	-	-	-	-
Gleicheniaceae	<i>Dicranopteris linearis</i> (Burm. f.) Underw.	-	+	-	+	-	+	+
Grammitidaceae	<i>Ctenopteris blechnoides</i> (Grev.) W.H. Wagner & Grether	+	-	-	-	-	-	-
Hymenophyllaceae	<i>Cephalomanes singaporeanum</i> Bosch	+	-	-	-	-	-	-
	<i>Microgonium</i> sp.	+	-	-	-	-	-	-
	<i>Selenodesmium obscurum</i> (Blume) Copel.	+	-	-	-	-	-	-
Lycopodiaceae	<i>Lycopodium cernuum</i> L.	-	+	+	+	-	+	-
Nephrolepidaceae	<i>Nephrolepis auriculata</i> (L.) Trimen	-	+	+	+	-	+	+
	<i>Nephrolepis</i> sp.	-	+	-	-	-	-	-
Polypodiaceae	<i>Goniophlebium percussum</i> (Cav.) W.H. Wagner & Grether	-	-	+	-	-	-	-
	<i>Drymoglossum piloselloides</i> (L.) Presl	-	-	-	-	-	-	+
	<i>Drynaria sparsisora</i> (Desv.) T. Moore	+	-	-	-	-	-	-
	<i>cf. Phymatosorus</i> sp.	-	-	-	-	-	-	+
Schizaeaceae	<i>Lygodium cf. longifolium</i> (Willd.) Sw.	+	-	-	-	-	-	-
	<i>Lygodium cf. flexuosum</i> (L.) Sw.	-	-	-	-	-	-	+
	<i>Lygodium</i> sp. 1	-	-	+	-	-	-	-
	<i>Lygodium</i> sp. 2	+	+	-	+	-	+	-
	<i>Schizaea dichotoma</i> (L.) Sm.	+	-	-	-	-	-	+
	<i>Schizaea digitata</i> (L.) Sw.	-	-	-	-	-	-	+

FAMILY	GENERA AND SPECIES	QUADRATS							
		NATURAL FOREST				MAN-MADE FOREST			
		GPFR	BTNR	OP	RP	RU			
Selaginellaceae	<i>Selaginella roxburghii</i> (Hk. & Grev.) Spring	+	+	-	-	-	-	-	-
	<i>Selaginella willdenowii</i> (Desv.) Baker	+	-	-	-	-	-	-	-
Thelypteridaceae	<i>Christella subpubescens</i> (Bl.) Holtt.	-	-	+	-	-	-	-	-
	<i>Cyclosorus</i> sp.	-	+	-	-	-	-	-	-
	<i>Mesophlebion beccarianum</i> (Ces.) Holtt.	+	-	-	-	-	-	-	-
	<i>Pronephrium rubicundum</i> (Alderw.) Holtt.	+	-	-	-	-	-	-	-
	<i>Pronephrium triphyllum</i> (Sw.) Holtt.	-	+	+	+	+	+	+	-
	<i>Sphaerostephanos heterocarpus</i> (Bl.) Holtt.	+	+	-	-	-	-	-	-
Vittariaceae	<i>Vittaria ensiformis</i> Sw.	-	-	+	-	-	-	-	-
	<i>Vittaria ensiformis</i> var. <i>latifolia</i> Holtt.	-	-	-	-	-	+	-	-
	<i>Vittaria elongata</i> Sw.	+	+	+	-	-	-	-	+
Woodsiaceae	<i>Diplazium crenatoserratum</i> (Bl.) T. Moore	-	+	-	-	-	-	-	-
	<i>Diplazium tomentosum</i> Bl.	+	-	-	-	-	-	-	-
	<b>Total number of species</b>	25	23	17	13	14			

GPFR	Gunung Pulai Forest Reserve, Johor
BTNR	Bukit Timah Nature Reserve, Singapore
OP	Oil palm plantation, Johor
RP	Rubber plantation, Johor
RU	Rubber plantation, Singapore

### BOOK REVIEW

**A MODERN MULTILINGUAL GLOSSARY FOR TAXONOMIC PTERIDOLOGY.** D.B. Lellinger. 2002. Pteridologia No. 3. Hardback. 264 pp., 15 figures (line drawings). ISBN 0-933500-02-5. American Fern Society, Inc. [www.amerfermsoc.org](http://www.amerfermsoc.org) Price US \$28.00 + postage.

The presentation of this book is clear and easy to follow. It comprises a numbered list of preferred terms and their definitions, with English, Spanish, French and Portuguese paragraphs for each term. Synonyms (about 100 for the c. 1000 distinct terms), antonyms and related terms are provided where applicable. Contents, introduction and comprehensive indices are provided also in each language. Finally, word lists of the terms defined in the book are offered for downloading from the American Fern Society web site for use as dictionaries in word-processing programs.

I will quote from the introduction: "No attempt has been made to include archaic or obsolete uses or terms. All terms are defined as I believe they are currently used or should best be used. ... I have eliminated terms from the glossary that are difficult or impossible to define." This is a worthy aim, but does imply that anyone looking for guidance to previously written fern descriptions may not find what they are seeking.

When I first scanned this book, I wrote down a list of terms, definitions and miscellaneous observations that 'hit a nerve'. Since then, I have gradually whittled down my initial objections. Some arose from my own misconceptions, and in this respect, the book has been useful to me. There is variation in the precision of definitions for some groups of terms. In the section on laminae, the definitions for 648 lobe and 655 segment are very precise, even to the selective use of "fully connate" (lobe) and "fully adnate" (segment), but definitions of 650 pinna, 651 pinnule and 652 pinnulet (a neologism) seem to be much less rigorous viz. for the latter "a petiolulate or sessile division of a pinnule that is at least narrowed at the base".

The characterisation of 613 phyllopodium as "that portion of the stipe" should perhaps be recast, to include the possibility that a rhizome outgrowth may instead be involved. The terms 677 anadromous and 678 catadromous are defined only in relation to a pinna, with the "basal pinnule and/or vein group of the pinna directed towards the frond apex [base]". However, 496 dromy is defined more generally, and hence more correctly by reference to "basal axes or veins" and their relationship to "the second larger order of axes". This latter phrase might be better as "the next higher order of axes". With regard to spore formation, tetrad is defined (no. 764), but diad, as in some apomictic ferns, is not.

Term 819 raphe refers to the rhizocarp of *Marsilea*, but rhizocarp is listed only as a synonym of 822 sporocarp. While on the subject of *Marsilea*, a definition is given for the specialised cells on the submerged lamina of 'certain species' (644 hydropote/hydropotes), but in the section on indument, I struggled to find any suitable term for the uniquely constructed hairs in this genus.

This book is aimed at the Americas, not only in the choice of languages, but also the fern genera cited for some of the terms. On balance, I recommend this book to professional pteridologists, but I feel that the amateur would have valued the addition of explanatory illustrations and some sample descriptions.

Peter D. Bostock

**MORPHOMETRIC ANALYSIS OF VARIATION AMONG THREE  
POPULATIONS OF *DORYOPTERIS LUDENS*  
(ADIANTACEAE: PTERIDOPHYTA) IN THAILAND**

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Keywords: Adiantaceae, *Doryopteris ludens*, cluster analysis, canonical discriminant analysis, multivariate analysis.

**ABSTRACT**

Morphological variation within populations and among populations was examined in three populations of *Doryopteris ludens* from western and peninsular Thailand. Sixteen quantitative characters of both vegetative and reproductive characters were scored. The field data were analysed by means of cluster analysis and various discriminant analyses. Cluster analysis and canonical discriminant analysis indicated two groups. It is consequently concluded that there are two morphological varieties which that can be distinguished on the basis of sporangium length, sporangium width, fertile-frond sinus-depth, fertile-lamina width and habitat. A conventional identification key is provided, which is based on fertile-frond sinus-depth, sporangium length, and substrate conditions.

**INTRODUCTION**

*Doryopteris* is one of the smaller genera of the Pteridophytes. Tryon (1942) included 26 species in his revision of the genus. He also noted that *Doryopteris* is terrestrial, usually growing in rather dry, rocky places. Some species are extremely xeromorphic. Of the 26 species, there is only one species in Thailand, i.e. *Doryopteris ludens* (Wall. ex Hook.) J. Sm. as was enumerated in *Flora of Thailand*, volume 3 part 2 (Tagawa & Iwatsuki, 1985). This species is extremely variable in leaf form. The slender, elongate rhizome separates it from all other reticulate-veined species (Tryon, 1942) and it also differs from the closely related species *D. pedata* (L.) Fée in having a terete stipe. Geographically, this species is Asiatic, since its present distribution is confined to Myanmar, India, southern China and the Malay Peninsula, whilst the majority of *Doryopteris* species are American.

Preliminary studies of herbarium specimens deposited at the following herbaria (abbreviations according to Holmgren *et al.*, 1990):- Bangkok Forest Herbarium (BKF); the Professor Kasin Suvatabhandhu Herbarium, Department of Botany, Chulalongkorn University, Thailand (BCU); the Royal Botanic Gardens, Kew Herbarium (K) and The Natural History Museum, U.K. (BM), suggested that two forms of this species probably occurred, the normal and the dwarf forms. The normal form has a wider distribution throughout the country, occurring naturally in calcareous soils, in shady places in the dry evergreen forest, whilst the dwarf form is confined to the calcareous rocks of the limestone hills or limestone islands in peninsular Thailand. The specimens collected from Langkawi Island, Malaysia, and deposited at Kew

herbarium match well with this dwarf form. However, some additional field studies in peninsular Thailand revealed some morphological variations in characters related to size of frond within these dwarf form populations. There were still some overlaps in stipe length, lamina width and lamina length etc. between normal and dwarf forms, and so it remained unclear whether two forms could be recognized within this species.

The present study is aimed at clarifying the taxonomic status of these two morpho-ecological forms of *D. ludens* by determining the levels of intra- and inter-population variation in the Thai populations.

## MATERIALS AND METHODS

### Plant materials

Field collections of *D. ludens* were made during the rainy season to permit collection of complete specimens of both fertile and sterile fronds. Eighty-five specimens from three populations were sampled; the location, ecology and number of specimens are listed in Table 1. Sixteen quantitative characters of both vegetative and reproductive structures were measured or counted (Table 2).

**TABLE 1:** Location, ecology and number of specimens of the three populations of *Doryopteris ludens* in Thailand.

	Population	Location	Ecology	Number of specimens
1	Tub Sakae District, Prachuap Khiri Khan Province	Western Thailand	Calcareous soil in shady places in dry evergreen forest	30
2	Had Chao Mai District, Trang Province	Peninsular Thailand	Rock crevices, exposed or partially shaded in limestone hill	30
3	Muang District, Phangnga Province	Peninsular Thailand	Rock crevices, or on humus-rich rocks, exposed or partially shaded in limestone islands	25

### Specimens examined

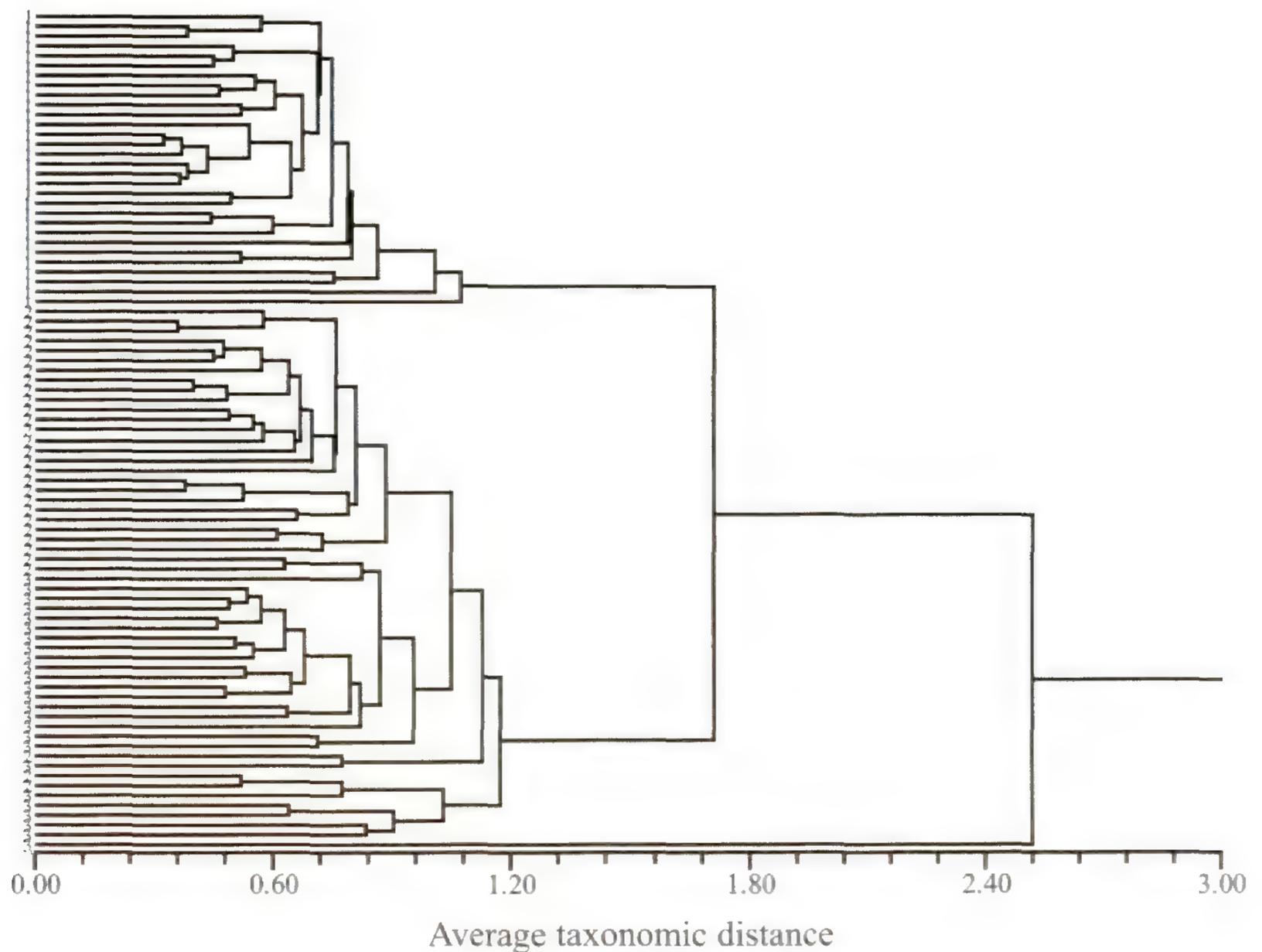
#### a. Normal form

**Habitat:** Terrestrial in tropical or evergreen forests at low or medium altitudes.

**Altitude :** 100-1500 m.

**Distribution:** India: Type: Wallich 88 (K); Isotype: Cuming 238 (K)

**Voucher:** Thailand: North: *R. Geesink* & *C. Phengklai* 5949 (BKF), *E. Hennipman* 3029 (BKF), *A.F.G Kerr* 11365 (BK), *Winit* 1074 (BKF); North-Eastern: *T. Boonkerd* 23, 269 (BCU), *J.F. Maxwell* 76-325 (BK), *M. Tagawa*, *K. Iwatsuki* & *N. Fukuoka* 1254 (BKF); Central: *Murata*, *Phengklai*, *Nagamasu* & *Nantasaen* T-51409(BKF), *J.F. Maxwell* 73-522 (BK), *A.F.G Kerr* 6029 (BK); East: *J.F. Maxwell* 74-978(BK), *W. Somprasong* 155 (BK); Western: *K. Chandraprasong* 61 (BK), *K. Larsen* & *S.S. Larsen* 33971 (BKF), *A. Marcan* 2696 (BM), *Put* 1430 (BK), *T. Boonkerd* 1122 (BCU); Peninsular: *Ch. Charoenphol*, *K. Larsen* & *E. Warncke* 3634 (BKF), *E. Smith* 2418A (BM), *Put* 1027, 1636, 3206 (BK, K),



**Figure 1.** Dendrogram of *Doryopteris ludens* specimens

***b. Dwarf form***

**Habitat:** Terrestrial in rock crevice or on humus rich rock in limestone islands or limestone hill.

**Altitude :** sea level to 250 m.

**Distribution:** Malaysia: Langkawi Island: *H.C. Robinson s.n. (K)*

**Voucher:** Thailand: South-Eastern: *E. Smith 2417A (BM)*; Western: *K. Larsen & S.S. Larsen 33688 (BKF)*, *Put 250 (BK, BM, K)*; Peninsular: *A.F.G Kerr 11365 (BK, K)*, *Rabil 131(BK, K)*, *T. Shimizu, N. Fukuoka & A. Nalampoon 7996 (BKF)*, *T. Boonkerd 151, 1443(BCU)*

**Data collection and multivariate analyses**

To determine patterns of variation in *D. ludens* both *a priori* and *a posteriori* grouping systems were examined. First, the pattern of variation was examined by cluster analysis using the average taxonomic distance among the 85 specimens (Rohlf & Sokol, 1965). A sequential, agglomerative, hierarchical and nested (SAHN) clustering nested technique (Sneath & Sokal, 1973) was performed using the unweighted pair-group method with arithmetic averages (UPGMA) which is available in NTSYS-pc package version 2.0K (Rohlf, 1998). The purpose of this analysis was to place individual specimens (N = 85) into groups (clusters) suggested by the data, but not defined *a priori*. Second, to determine whether morpho-ecological patterns existed from calcareous soil to calcareous rocks, each specimen was assigned to an *a priori* group based on its occurrence in natural habitat.

The SPSSpc-FW (Anonymous, 1997) was used to perform univariate analysis, stepwise discriminant analysis, classification discriminant analysis and canonical discriminant analysis. Stepwise discriminant analysis was used to select a subset of characters that maximized differences among the *a priori* groups. Correct classification rates were used as indicators of separation among the groups. Canonical discriminant analysis was used as a dimension reduction technique to facilitate visualization of the results of the multivariate analysis.

## RESULTS

### Patterns of variation among specimens of *D. ludens*

The SAHN technique generated a dendrogram which split the specimens into two groups (Figure 1). Specimens classified as group 1 in the cluster analysis consisted of all *D. ludens* from only population 1, whilst group 2 included members from both population 2 and population 3 which are rather separated into two subgroups. These two groups matched the morpho-ecological patterns of this species, i.e. normal form and dwarf form. However, the separation of group 2 into two subgroups suggested intra- and inter-population variation in the dwarf populations. Accordingly, three-clustering grouping were used in subsequent analysis as *a posteriori* groups.

Sixteen characters were determined by stepwise discriminant analysis to be important in discriminating between the three groups. The following nine characters:- 4, 5, 6, 8, 9, 11, 13, 14, 15 were selected as important for giving the best separation of the groups (Table 3). In total, 97.6% of the specimens were classified correctly. These classification rates are extremely high considering that variation within the three populations existed.

Ordination of the 85 specimens by canonical discriminant analysis was presented on the two canonical axes (Figure 2). This shows population 1 clearly separated from closely related population 2 and population 3 on axis 1. Thus the two morpho-ecological forms of *D. ludens* appear distinct. The nature of the group differences is characterized by the within-canonical structure (Table 3). Canonical variable 1 (axis 1) is most highly associated with characters 14, 15, 6, 5, 7, 3, 16 and 12 in descending order of the absolute values of the correlations (Table 3). The canonical correlation of the first canonical discriminant function is 98% correlated with all the variables and the variance explained by it is 93.5%. Thus this axis is effective for separating the two morpho-ecological groups of *D. ludens*.

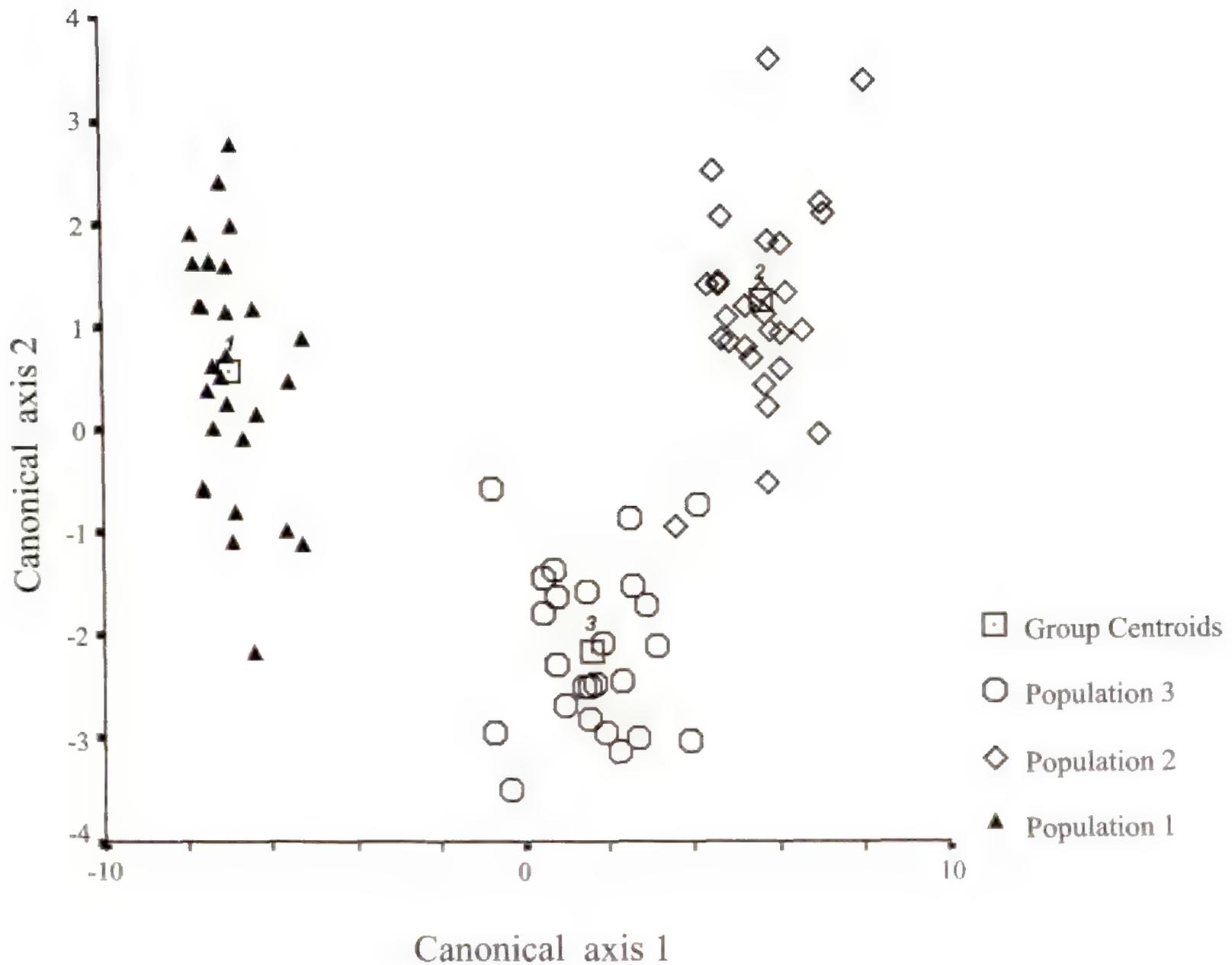
The F-values (Table 3) indicate by their magnitude the relative order of importance of the characters in general. It is clear that the F-values almost reflect the association of characters with canonical axis 1 because of its high correlation and high variance explained. Basic statistics of the three groups are also summarized in Table 3. It can be concluded that the vegetative characters of the normal form (population 1) were generally larger than the dwarf form (population 2 and 3). In contrast, the reproductive characters of the dwarf form were bigger than the normal form. In general, the means of the most important characters were significantly different, especially the four most important characters for axis 1 as can be seen from boxplots (Figure 3).

## DISCUSSION

The results of cluster analysis, and canonical discriminant analysis support the recognition of separating the three populations of *D. ludens* into two distinct entities, probably as two varieties. The four most important characters (Table 3) that separate

TABLE 2. Morphological characters used in the multivariate analysis of *Doryopteris ludens*

	Number	Character	Details of measurements and counts
Vegetative	1	fertile stipe diameter (mm)	diameter at base of stipe of fertile frond
	2	sterile stipe diameter (mm)	diameter at base of stipe of sterile frond
	3	fertile lamina length (cm)	length of lamina of fertile frond
	4	fertile lamina lobe number	numbers of lobes of lamina of fertile frond
	5	fertile lamina width (cm)	width of lamina of fertile frond
	6	fertile frond sinus depth (cm)	distance between margin and base of sinus of fertile frond
	7	fertile stipe length (cm)	length of stipe of fertile frond
	8	sterile lamina length (cm)	length of lamina of sterile frond
	9	sterile lamina lobe number	numbers of lobes of lamina of sterile frond
	10	sterile lamina width (cm)	width of lamina of sterile frond
	11	sterile frond sinus depth (cm)	distance between margin and base of sinus of sterile frond
Reproductive	12	sterile stipe length (cm)	length of stipe of sterile frond
	13	annulus thick ( $\mu\text{m}$ )	distance from top to base of an annulus cell situated at the top of sporangium
	14	sporangium length ( $\mu\text{m}$ )	longest distance measured from base to top of sporangium (without stalk)
	15	sporangium width ( $\mu\text{m}$ )	longest distance measured from side to side of sporangium at the equatorial axis
	16	spore diameter ( $\mu\text{m}$ )	length of spore from polar view or polar diameter



**Figure 2.** Canonical discriminant analysis

these two varieties are sporangium length (14), sporangium width (15), fertile-frond sinus-depth (6), and fertile-lamina width (5). However, fertile-frond sinus-depth (6) and fertile-lamina width (5) tend to be more important in the field for separating normal and dwarf forms of *D. ludens* as sporangium length (14) and sporangium width (15) are microscopic characters, only suitable for laboratory herbarium determination. These two vegetative characters are characters of leaf dissection as mentioned in Tryon (1942) in his revision of the genus. He noted that most of the species are quite variable in leaf dissection and should not be used alone as a diagnostic character in key construction, even as infraspecific determination, unless supported by additional characters. However, Tryon (1942) recognized the value of the sporangium stalk-length together with the leaf dissection characters to separate the species.

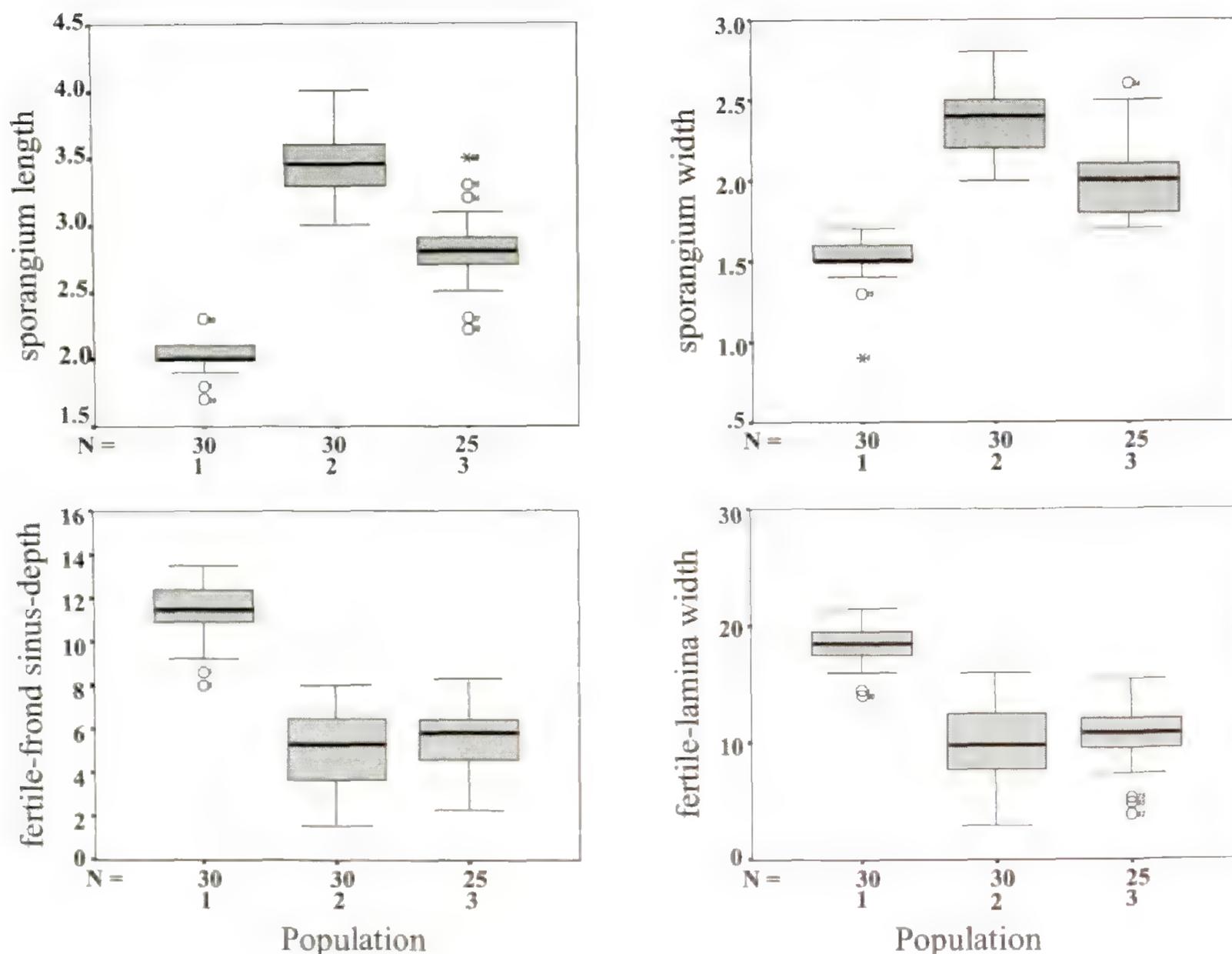
Baum and Bailey (1994) used a series of discriminant analyses to determine taxonomic status of *Hordeum caespitosum* Scribner from different geographical ranges. They pointed out that for *Hordeum* a group of characters must be used together for identification, at least of the most important ones in the above sense. Speer and Hilu (1999) evaluated taxonomic status and determined quantitatively the importance of morphological characters that contribute to the discrimination between var. *latiusculum* (Desv.) W.C. Shieh and var. *pseudocaudatum* (Clute) A. Heller of Bracken fern, *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) which is usually treated as a single species. They concluded that the treatment of the eastern North American bracken as var. *latiusculum* and var. *pseudocaudatum* seemed justifiable from the results of their study.

**TABLE 3:** Pooled within-canonical structure and F-values with their probabilities. Correlations between the two canonical variables and the original variables. Summary of mean, SD in the three populations of *Doryopteris ludens*

Character	F-value	Prob.	Axis 1	Axis 2	Population 1 mean SD	Population 2 mean SD	Population 3 Mean SD
1. fertile-stipe diameter <sup>a</sup>	43.83	0.00	0.01	0.18*	1.89 0.18	1.36 0.25	1.40 0.28
2. sterile-stipe diameter <sup>a</sup>	15.91	0.00	-0.13	0.41*	1.32 0.21	1.33 0.18	1.05 0.23
3. fertile-lamina length <sup>a</sup>	143.58	0.00	-0.19*	0.16	20.79 2.27	9.53 3.23	11.25 2.64
4. fertile-lamina-lobe number	2.67	0.75	0.04	-0.09*	13.67 2.26	16.13 5.68	17.00 7.94
5. fertile-lamina width	87.48	0.00	-0.26*	0.25	18.26 1.88	9.76 3.43	10.33 2.70
6. fertile-frond sinus-depth	151.80	0.00	-0.34*	0.32	11.47 1.31	5.14 1.85	5.59 1.42
7. fertile-stipe length <sup>a</sup>	44.83	0.00	-0.22*	0.10	39.34 12.04	16.68 6.95	24.74 8.19
8. sterile-lamina length	113.23	0.00	-0.28	0.43*	14.50 2.07	8.20 1.52	7.58 2.18
9. sterile-lamina-lobe number	52.96	0.00	0.19	0.29*	7.03 1.16	15.67 3.47	9.92 4.59
10. sterile-lamina width <sup>a</sup>	1.42	0.25	-0.04	0.14*	10.83 2.02	7.89 1.55	9.18 2.23
11. sterile-frond sinus-depth	59.92	0.00	-0.19	0.41*	5.66 1.57	3.15 0.71	2.46 0.99
12. sterile-stipe length <sup>a</sup>	26.02	0.00	-0.10*	0.10	22.48 6.91	13.25 4.95	13.16 4.71
13. annulus-thick	230.33	0.00	0.41	0.46*	5.04 0.56	9.01 0.86	6.69 0.72
14. sporangium-length	294.69	0.00	0.48*	0.26	2.03 0.12	3.47 0.22	2.82 0.32
15. sporangium-width	146.61	0.00	0.34*	0.13	1.50 0.14	2.40 0.20	2.02 0.25
16. spore-diameter <sup>a</sup>	150.92	0.00	0.16*	-0.04	5.39 0.71	9.40 1.14	8.13 0.83

<sup>a</sup> : character not used in the stepwise analysis,

\* : largest absolute correlation between each variable and any discriminant function



**Figure 3.** Boxplots of the four most important characters

**Key to identify the infraspecific taxa of *D. ludens*.**

Fertile-frond sinus-depth more than 7 cm; sporangium length 1.9-2.1 mm; plant growing in calcareous soils, in dense dry evergreen forest var. A (*ludens*)  
 Fertile-frond sinus-depth less than 7 cm; sporangium length 2.5-3.7 mm; plant growing in rock crevices, exposed or partially shaded var. B

**CONCLUSION**

The results provided justification for the recognition of infraspecific variation among the three populations of *D. ludens*. In most cases they can be distinguished morphologically by their sporangium length, sporangium width, fertile-frond sinus-depth, fertile-lamina width and by their habitats (calcareous soils or calcareous rocks). However, this study is exploratory and further verification is required.

**ACKNOWLEDGMENTS**

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## THE CURRENT STATUS AND DISTRIBUTION OF THE FALKLAND ISLANDS PTERIDOPHYTE FLORA

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Key words: Falkland Islands, pteridophyte, fern, clubmoss, conservation, distribution, Lycopodiopsida, Pteropsida

### ABSTRACT

The Falkland Islands are an archipelago of 782 islands situated in the South Atlantic Ocean. They have a relatively depauperate native flora of vascular plants comprised of 171 species, 18 of which are pteridophytes. The pteridophyte flora includes a further three non-native taxa. Current knowledge of all pteridophyte taxa occurring in the Falkland Islands is reviewed and the first detailed data on their distribution throughout the archipelago are presented.

### INTRODUCTION

The Falkland Islands are an archipelago of 782 islands situated in the South Atlantic Ocean approximately 520 kilometres east of mainland South America, and with a total land area of *c.* 12,200 km<sup>2</sup>. The climate is cool temperate oceanic, with a relatively modest seasonal variation. Temperatures are never high but are maintained at a moderate level with a mean for January of 9.4°C and a mean for July of 2.2 °C, with ground frosts occurring throughout the year. The Islands are subject to almost continual strong winds that come mainly from the southwest. The mean hourly wind-speed of 8.5 ms<sup>-1</sup> does not vary appreciably throughout the year though there is a greater frequency of stronger winds in spring and early summer. Rainfall is low with a mean annual precipitation, during the period 1944-1978, at Stanley of 640 mm, though the mean annual rainfall received tends to decline towards the south and west. Rainfall is lowest in spring and this combined with the strong winds reduces plant growth (McAdam, 1985; Summers & McAdam, 1993). Climatic variation across the Falkland Islands archipelago is poorly understood but climatic gradients are likely to be an important factor in determining the distribution of some plant species, notably some pteridophytes.

The topography of the islands is not extreme with the landscape being generally hilly and the tallest mountain, Mt. Usborne on East Falkland, is only 705 m high. A typical Falkland soil has a pH in the range of 4.1 to 5.0 and comprises a shallow (typically no deeper than 38 cm) peaty horizon overlying a compact, poorly drained silty clay subsoil. Mineral soils occur in areas wherever the underlying geology is exposed, particularly on mountain tops and in coastal areas. The main vegetation of the Falkland Islands is acid grassland dominated by *Cortaderia pilosa* (d'Urv.) Hack. and dwarf shrub heath dominated by *Empetrum rubrum* Vahl ex Willd., but other vegetation types of more limited extent may be locally important particularly around the coasts.

There is no native tree cover. The main land use is sheep farming which is managed on an extensive, rangeland system. As a result, there are few areas in the islands that are not subject to grazing pressure for at least part of the year, though the potential negative effects of this for the pteridophyte flora appear to be minimal.

### THE PTERIDOPHYTE FLORA: AN OVERVIEW

The 21 species of pteridophyte found in the Falkland Islands comprise a small but significant component of the 346 vascular plant species currently recorded for the archipelago. Of these, 18 species are native and represent 10.5% of the 171 native plant species. The pteridophyte flora is spread between two classes (Lycopodiopsida and Pteropsida), 10 families and 15 genera. The lesser of the classes, the Lycopodiopsida, comprises one family, two genera and three species, all of which are native. The Pteropsida come from nine families, 13 genera and 18 species, two genera and three species of which are non-native in origin having been introduced as garden plants. The Falkland Islands have no endemic pteridophytes, though *Polystichum mohrioides* (Bory) C. Presl. is restricted to the Falkland Islands and South Georgia and can be considered near endemic.

A further species, *Schizaea fistulosa* Labill., has previously been reported for the Falkland Islands (Gaudichaud, 1825 cited in Moore, 1968). However, this record is based on the flimsiest of evidence and significant doubt is now cast on its validity. It appears the one and only record of this species for the Falkland Islands (Gaudichaud, 1825) was the result of a vague recollection of it having been encountered there. Given that no other records of this species in the Falkland Islands exist and given that Gaudichaud's travels took him to places other than the Falkland Islands and that no herbarium specimen exists to support his claim, it now seems reasonable to assume that Gaudichaud was in error in reporting the species from the Falkland Islands and that the species has never been part of the flora (Skottsberg, 1913; Broughton, 2000).

### DISTRIBUTION OF PTERIDOPHYTE TAXA

The Falkland Islands pteridophyte flora contains an interesting mix of common and rare species. The common species, such as *Blechnum penna-marina* (Poir.) Kuhn and *B. magellanicum* (Desv.) Mett., can generally be found wherever suitable habitat exists. The rare flora however, is much more exacting in its requirements, and is consequently vulnerable to disturbance and the destruction of populations. Clear trends can be discerned in the distribution of certain components of the pteridophyte flora both in terms of geography and ecology (though in many cases these are likely to be linked).

Four (22%) of the native pteridophyte species - *Adiantum chilense* Kaulf., *Blechnum cordatum* (Desv.) Hieron, *Rumohra adiantiformis* (Forst. f.) Ching and *Hymenophyllum tortuosum* Hook. & Grev. - are currently known to occur only on West Falkland and the associated islands. Both *Blechnum cordatum* and *Rumohra adiantiformis* appear to be restricted to the northwest of West Falkland. Although variations in climate across the Falkland Islands archipelago are poorly understood it is known that West Falkland tends to benefit from a milder, drier and sunnier climatic regime, particularly in the northwest. As a result climate is likely to play a significant role in determining the distribution of these taxa. In comparison only one species, *Botrychium dusenii* (Christ) Alston, is currently known only from East Falkland. However, despite the rarity of this species the authors believe that it is likely to prove more widespread. It is perhaps no coincidence that the longest known population of this species is less than 3 km from the capital Stanley. The alien pteridophyte flora is also known only from the islands of West

Falkland. As all three species are likely to have been introduced as garden plants this may be a reflection of where they were first introduced into the Falkland Islands. There is certainly evidence to suggest that wild populations of *Dryopteris dilatata* (Hoffm.) A. Gray may be descended from material cultivated in the gardens on West Point Island.

With the exception of members of the Blechnaceae and the Lycopodiaceae most pteridophyte taxa appear to be largely absent from the dominant vegetation types of dwarf shrub heath and acid grassland, and this becomes more pronounced the further inland travelled. Even where species do occur in these dominant vegetation types, again with the exception of the Blechnaceae and Lycopodiaceae, they are generally so scarce as to suggest that some other ecological factor must be playing a significant role in determining distribution. In such species there is either a strong association with upland rocky habitats or with lowland habitats in close proximity to the coast. The distribution of the former group of species largely reflects the availability of suitable rock outcrops, and where suitable conditions occur in the lowlands they may be found here also, whilst the latter, which are often at the southern limits of their distribution in the Falkland Islands, probably require a milder climatic regime which can only be found in close proximity to the sea.

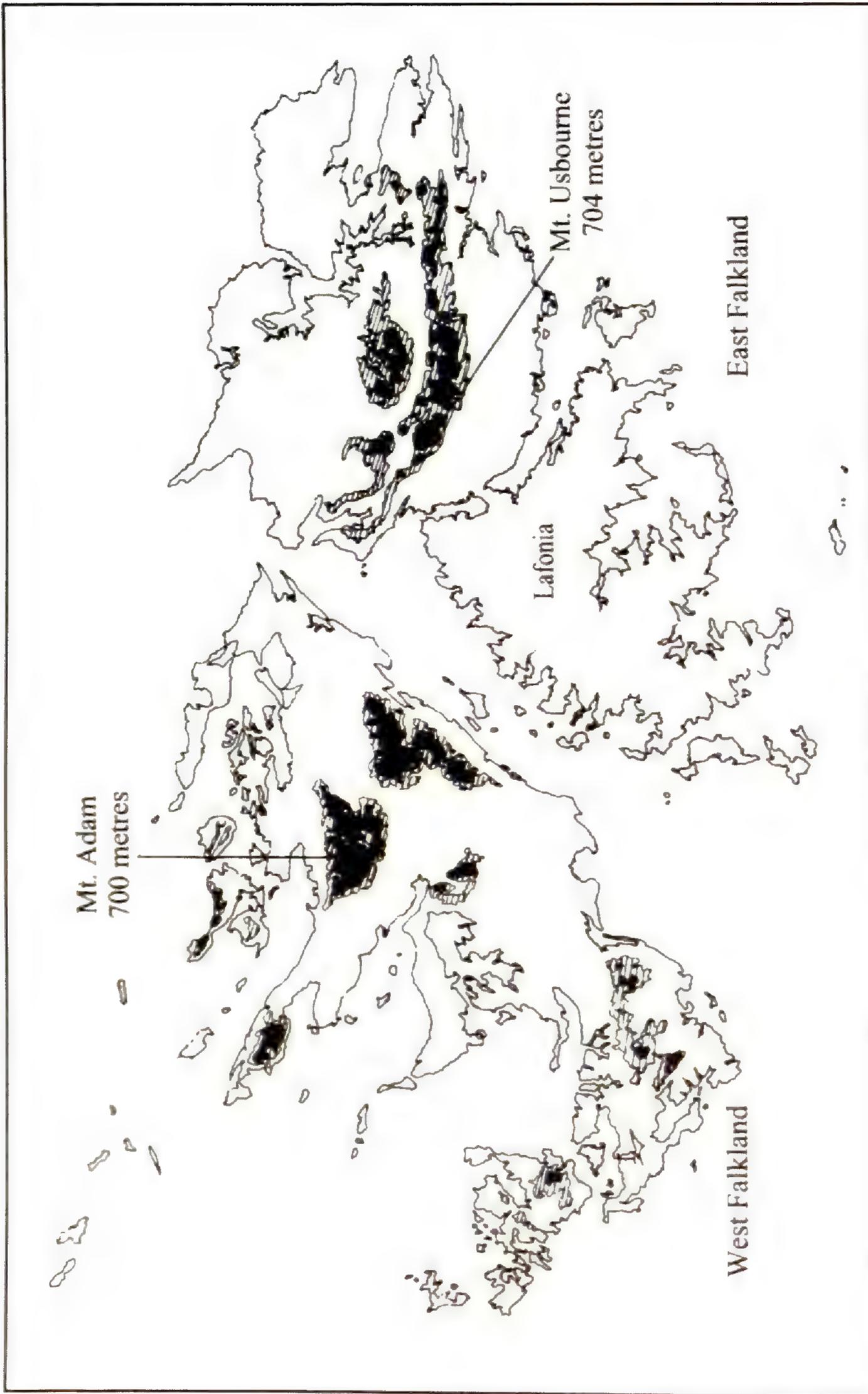
It is only the common members of the Blechnaceae and Lycopodiaceae that are particularly widespread and occur in a wide range of habitats, and only *Blechnum penna-marina* can be considered a true generalist, being almost ubiquitous in all terrestrial habitats except wetlands proper, but including marginal vegetation. As a result *Blechnum penna-marina* is one of the most abundant plant species present in the Falkland Islands.

Pulling together these data on the geography and ecology of Falkland Islands pteridophyte taxa it can be concluded that the highest diversity of pteridophyte taxa can be found where the coasts and lowlands meet rocky upland areas. This is clearly illustrated by comparing Figs. 1 and 2. Taken together, these show that the richest 10 km grid squares for pteridophytes are those in which the two highest peaks, Mt Adam (grid square TC88) and Mt Usborne (UC77), occur in close proximity to lowland areas. Ten pteridophyte taxa have been recorded for each of these two grid squares. Species diversity is lowest on the smallest islands and in much of the Lafonia region. Lafonia is notable for being low-lying and for the general absence of rocky outcrops, and it is this that is probably largely responsible for the low pteridophyte diversity. Another important factor may be summer drought stress and this is almost certainly responsible for the extreme scarcity of *Blechnum magellanicum* in this area (Figure 9).

### CONSERVATION RELEVANCE

Falkland Islands pteridophytes as a group are of great concern to the national conservation strategy. Of the 28 plant species protected by law in the Falkland Islands (Falkland Islands Government, 1999) six (21% of protected plants and 33% of native pteridophytes) are pteridophytes (Table 1). Likewise, six species are listed as threatened (27% of threatened taxa and 33% of native pteridophytes, Table 1) in the National Red Data List (Broughton & McAdam, 2002) and *Grammitis poeppigiana* (Mett.) Pic. Serm. may be threatened but is currently listed as Data Deficient.

A further species, *Polystichum mohrioides*, although not currently threatened, is also of conservation relevance. This species is believed to be restricted to South Georgia and the Falkland Islands and, as a result, the Falkland Islands may be responsible for a significant proportion of the world population.



**Figure 1.** Map of the Falkland Islands archipelago illustrating the major upland areas and the highest peaks on East Falkland (Mt. Usbourne) and West Falkland (Mt. Adam).



**TABLE 1.** Threatened Falkland Islands' pteridophytes

<b>Species</b>	<b>National IUCN threat category</b>	<b>Protected by law</b>
<i>Adiantum chilense</i>	Endangered	yes
<i>Blechnum cordatum</i>	Vulnerable	yes
<i>Botrychium dusenii</i>	Vulnerable	yes
<i>Huperzia fuegiana</i>	Endangered	yes
<i>Ophioglossum crotalophoroides</i>	Vulnerable	yes
<i>Rumohra adiantiformis</i>	Endangered	yes
<i>Grammitis poeppigiana</i>	Data Deficient	no

At present the conservation of threatened pteridophytes has progressed little beyond the recognition that they are of concern and the provision of legal protection. Much work is urgently required, particularly survey work, to locate and assess all surviving populations, research to determine their precise ecological niche within the Falkland Islands, publicity to raise the awareness of the identity and status of threatened pteridophytes on the farms in which they occur, the adequate protection of vulnerable populations and where necessary positive conservation action to ensure the survival and expansion of vulnerable populations. As a result the threatened pteridophytes of the Falkland Islands will provide an interesting conservation challenge for the future.

### SPECIES ACCOUNTS

Accounts of all pteridophyte taxa present in the Falkland Islands are provided below. Nomenclature follows Zuloaga & Morrone (1996) and Pryer *et al.*, (2001) and species are arranged by class and then alphabetically by family and genus. Reference is made to a voucher specimen held by Kew (K), or if not available, then the Natural History Museum (BM). National Red Data List categories, where assigned, follow IUCN (2001) and more detail on threatened pteridophyte taxa can be found in Broughton & McAdam (2002). Legal protection is provided by inclusion in the *Conservation of Wildlife and Nature Ordinance 1999* (Falkland Islands Government, 1999).

The maps presented illustrate the known distribution of each native species. They use all available records that can be assigned to one 10 km grid square (a lack of precision in some of the oldest records meant they could not be mapped). The maps only indicate presence in a grid square and the lack of a record from any particular grid square should not be used to infer absence of the species. However, trends can be identified in the distribution of many species and these are outlined in the species accounts and earlier sections.

**LYCOPODIOPSIDA**  
**LYCOPODIACEAE**

1. *Huperzia fuegiana* (Roiv.) Holub 1985, Folia Geobot. Phytotax. 20: 72. Moore 1983: 46 as *Huperzia selago*. Figure 3.

**Habitat:** Exposed situations without shrub overgrowth, such as rocky ledges, peaty hummocks around boulders, and sites where the growth of dwarf shrubs and other vegetation is low and thinned by the presence of shallow underlying rocks.

**Altitude:** 0-300 m (and probably higher).

**Distribution:** Very locally distributed across the larger islands (Figure 3).

**Status:** Native and rare.

**National Red Data List category:** Endangered.

**Legal Status:** Nationally protected.

**Voucher:** Moore 533 (K).

2. *Lycopodium confertum* Willd. 1810, Sp. Pl., ed. 4, 5: 27. Moore 1983: 46. Figure 4.

**Habitat:** More open facies of *Empetrum rubrum* heathland and *Cortaderia pilosa* acid grassland.

**Altitude:** 0-650 m.

**Distribution:** Widespread across the larger islands (Figure 4).

**Status:** Native and scarce. This species seems to be naturally less abundant than the next species and this may be a result of the creeping growth-form, which may make plants less able to compete with other vegetation and thus dependent on more open conditions.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** Moore 587 (K).

3. *Lycopodium magellanicum* (P. Beauv.) Swartz 1806, Syn. Fil. 180. Moore 1983: 46. Figure 5.

**Habitat:** *Empetrum rubrum* heathland, *Cortaderia pilosa* acid grassland and inland rock habitats.

**Altitude:** 0-610 m

**Distribution:** Widespread across the islands (Figure 5).

**Status:** Native and common.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** Moore 716 (K).

**PTEROPSIDA**  
**ADIANTACEAE**

1. *Adiantum chilense* Kaulf. 1824, Enum. Fil. 207 var. *chilense*. Moore 1968: 46. Figure 6.

**Habitat:** Moist fissures and overhangs on sea cliffs, shaded from the mid-day sun, and within a few metres of the sea.

**Altitude:** c. 1 m.

**Distribution:** Very locally distributed on West Falkland (Figure 6). Essentially a species of warmer climes it is at the southern and eastern limits of its natural distribution in the Falkland Islands. It is currently only known from Saunders Island though it has been recorded more widely in the past.

**Status:** Native and rare.

**National Red Data List category:** Endangered.

**Legal Status:** Nationally protected.

**Voucher:** *Vallentin v.1911* (K).

#### ASPLENIACEAE

1. *Asplenium dareoides* Desv. 1811, Ges. Nat. Freunde Berl. Mag. 5: 322. Moore 1983: 56. Figure 7.

**Habitat:** Shady, humid crevices in rock outcrops and amongst boulders.

**Altitude:** 155-460 m.

**Distribution:** Locally distributed across the uplands of the larger islands (Figure 7).

**Status:** Native and rare. Despite the apparent rarity of this species there is no reason to believe it is threatened. The preference for upland rocky habitats ensures the species is not currently threatened by human activities. The species may be under-recorded and more survey work is required.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Vallentin xi.1910* (K).

2. *Phyllitis scolopendrium* (L.) Newman 1844, Hist. Brit. Ferns ed. 2: 10. Moore 1968: 48.

**Habitat:** Inland rock.

**Altitude:** Not known.

**Distribution:** Very locally distributed in West Falkland. Two records exist, Mount Philomel area, West Falkland and Pebble Island (UD01).

**Status:** Introduced, very rare. Last recorded 1994.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Vallentin* (K).

#### BLECHNACEAE

1. *Blechnum cordatum* (Desv.) Hieron 1908, Hedwigia 47: 239. Moore 1968: 50-51 as *Blechnum chilense*. Figure 8.

**Habitat:** *Empetrum rubrum* heathland and *Blechnum magellanicum* stands.

**Altitude:** c. 60 m.

**Distribution:** Locally distributed in northwest West Falkland (Figure 8). The species is at the southern and eastern limits of its natural distribution in the Falkland Islands.

**Status:** Native and rare to scarce.

**National Red Data List category:** Vulnerable.

**Legal Status:** Nationally protected.

**Voucher:** *Moore 858* (K).

2. *Blechnum magellanicum* (Desv.) Mett. 1856, Fil. Lechl. 1: 14. Moore 1983: 60. Figure 9.

**Habitat:** Present in most terrestrial communities except wetlands and communities subject to drought stress. Large, dense stands are common at the base of rocky outcrops where water requirements are most easily met, and where humidity is relatively uniform.

**Altitude:** 0-300 m.

**Distribution:** Widespread across the islands. Largely absent from areas subject to summer drought stress such as the Lafonia region of East Falkland (Figure 9).

**Status:** Native and common.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Moore 771* (K).

**3. *Blechnum penna-marina*** (Poir.) Kuhn 1868, *Filic. Afr.* 92. Moore 1983: 60. Figure 10.

**Habitat:** This species is a generalist found in all vegetation communities, except wetlands, but including marginal vegetation. On drier soils this species can dominate to the exclusion of all other taxa.

**Altitude:** 0-705 m

**Distribution:** Near ubiquitous throughout (Figure 10) and probably absent only from Beauchêne Island.

**Status:** Native and very common.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Moore 739* (K).

#### DRYOPTERIDACEAE

**1. *Dryopteris dilatata*** (Hoffm.) A. Gray 1848, *Man. Bot. North. U.S.* 631. Moore 1968: 49.

**Habitat:** Not known, probably associated with habitation.

**Distribution:** Very locally distributed in northwest West Falkland. The herbarium material from West Point Island (TD40) collected by Sladen (see below) and cited by Moore (1968) was of cultivated origin.

**Status:** Introduced and very rare, last recorded 1909-1911 but may still persist.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Sladen JB123/5* (BM).

**2. *Dryopteris filix-mas*** (L.) Schott 1834, *Gen. Fil.* 9. Moore 1968: 49.

**Habitat:** Not known.

**Distribution:** Very local, recorded from an unknown location in northern West Falkland.

**Status:** Introduced and very rare. Reported only once and voucher material was not collected (Wright, 1911). The record should perhaps be treated with some caution.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** None available.

**3. *Polystichum mohrioides*** (Bory) C. Presl. 1863, *Tent. Pteridogr.* 83. Moore 1968: 48-49. Figure 11.

**Habitat:** Crevices in rock outcrops and among boulders, more rarely in dwarf shrub heath.

**Altitude:** 10-600 m (commonest in the uplands).

**Distribution:** Locally distributed across the larger islands, particularly the uplands (Figure 11).

**Status:** Endemic to the Falkland Islands and South Georgia. The abundance of the species at any one site is dictated by the availability of suitable habitat, as a result it is generally scarce.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** Moore 924 (K).

4. *Rumohra adiantiformis* (Forst. f.) Ching 1934, Sinensia 5: 70. Moore 1968: 47. Figure 12.

**Habitat:** *Empetrum rubrum* heathland and *Blechnum magellanicum* stands, more rarely on coastal cliffs.

**Altitude:** 0-15 m.

**Distribution:** Very locally distributed in northwest West Falkland (Figure 12).

**Status:** Native and rare.

**National Red Data List category:** Endangered.

**Legal Status:** Nationally protected.

**Voucher:** Moore 860 (K).

#### GLEICHENIACEAE

1. *Gleichenia cryptocarpa* Hook. 1844, Sp. Fil. 1: 7. Moore 1983: 63. Figure 13.

**Habitat:** Occurring either as pure stands or in *Empetrum rubrum* heath and *Chilotrichum diffusum* scrub, it is most abundant where it occurs on loose sandy soils.

**Altitude:** 0-150 m.

**Distribution:** Locally distributed on West Falkland, only one location known on East Falkland (Figure 13).

**Status:** Native and locally common.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** Moore 787 (K).

#### GRAMMITIDACEAE

1. *Grammitis poeppigiana* (Mett.) Pic. Serm. 1978, Webbia 32 (2): 455. Moore 1983: 50 as *Grammitis magellanica* f. *nana*. Figure 14.

**Habitat:** Crevices on upland rock outcrops.

**Altitude:** 180-485 m.

**Distribution:** Very locally distributed in the uplands of the larger islands (Figure 14).

**Status:** Native and rare? The species may be under-recorded and more survey work is required.

**National Red Data List category:** Data Deficient.

**Legal Status:** Not protected.

**Voucher:** Corner 333 (K).

#### HYMENOPHYLLACEAE

1. *Hymenophyllum caespitosum* Gaudich. 1825, Annl. Sci. Nat. 5: 99. Moore 1983: 56 as *Serpyllopsis caespitosa*. Figure 15.

**Habitat:** Inland rock outcrops and on moist peat at the base of such outcrops. This species seems the most tolerant of the three *Hymenophyllum* taxa to desiccation, and consequently can be found in more exposed, drought-prone situations where the other two species are absent.

**Altitude:** 60-300 m.

**Distribution:** Widespread across the larger islands, commonest in the uplands (Figure 15). Based on current experience, further survey work is likely to reveal this species to be present on most upland rock outcrops.

**Status:** Native and common.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Moore 802b* (K).

**2. *Hymenophyllum falklandicum*** Baker 1874, in Hook. & Baker, Syn. Fil. ed. 2: 68. Moore 1983: 55. Figure 16.

**Habitat:** Moist shady niches on rock faces and amongst boulders, more rarely on moist peat in *Cortaderia pilosa* acid grassland.

**Altitude:** 0-515 m.

**Distribution:** Widespread across the larger islands, commonest in the uplands (Figure 16).

**Status:** Native and scarce.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Moore 802a* (K).

**3. *Hymenophyllum tortuosum*** Hook. & Grev. 1829, Icon. Fil. 2: 129. Moore 1983: 53. Figure 17.

**Habitat:** Inland rock outcrops.

**Altitude:** 155-396 m.

**Distribution:** Locally distributed in upland areas of northern West Falkland (Figure 17) and likely to prove more widespread than current data would suggest.

**Status:** Native and scarce.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** *Vallentin in 1909-11* (K).

#### OPHIOGLOSSACEAE

**1. *Botrychium dusenii*** (Christ) Alston 1960, Lilloa 30: 107. Moore 1983: 47. Figure 18.

**Habitat:** Short, open grassy turf and eroded areas on sandy soils near the coast.

**Altitude:** *c.* 3 m.

**Distribution:** Very locally distributed on East Falkland (Figure 18). Possibly overlooked at suitable sites elsewhere in the archipelago.

**Status:** Native and rare.

**National Red Data List category:** Vulnerable.

**Legal Status:** Nationally protected.

**Voucher:** *Moore 530* (K).

2. *Ophioglossum crotalophoroides* Walt. 1788, Fl. Carol. 256. Moore 1983: 47. Figure 19.

**Habitat:** On peaty soils in *Empetrum rubrum* heathland and *Cortaderia pilosa* acid grassland.

**Altitude:** 15-120 m.

**Distribution:** Very locally distributed across the islands (Figure 19).

**Status:** Native and rare.

**National Red Data List category:** Vulnerable.

**Legal Status:** Nationally protected.

**Voucher:** Moore 636 (K).

### WOODSIACEAE

1. *Cystopteris fragilis* (L.) Bernh. 1806, Neues J. Bot. 1 (2): 27. Moore 1983: 56. Figure 20.

**Habitat:** Moist shady crevices on rock outcrops.

**Altitude:** 0-100 m.

**Distribution:** Locally distributed across the islands (Figure 20). The distribution of the species is probably severely limited by a requirement for calcium and for conditions free from summer drought. Such conditions are uncommon in the Falkland Islands.

**Status:** Native and scarce.

**National Red Data List category:** None.

**Legal Status:** Not protected.

**Voucher:** Moore 639 (K).

### ACKNOWLEDGEMENTS

This work would not have been possible without funding from the UK Government through the Darwin Initiative programme (Department for Environment, Food and Rural Affairs). We acknowledge the Falkland Islands Government for providing funding that has helped support the post of a full-time botanist in the Falkland Islands, allowing a third season of field research. We also commend them for acting to update the protected species legislation in line with the National Red Data List. Finally, we wish to thank all those who have contributed records to the vascular plant recording scheme.

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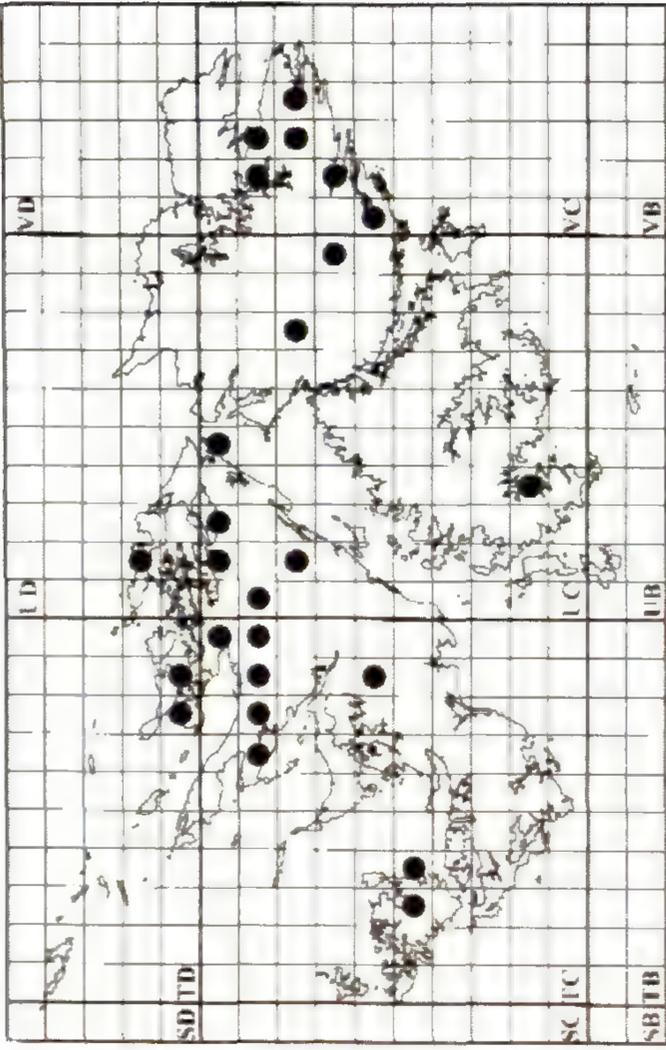


Figure 4. *Lycopodium confertum*

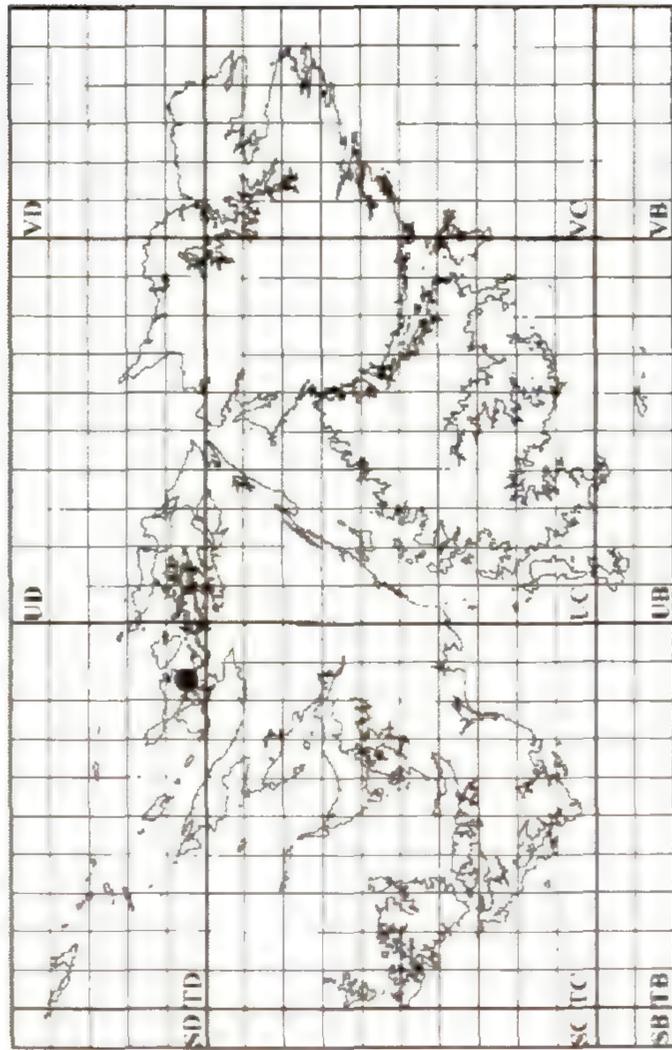


Figure 6. *Adiantum chilense*

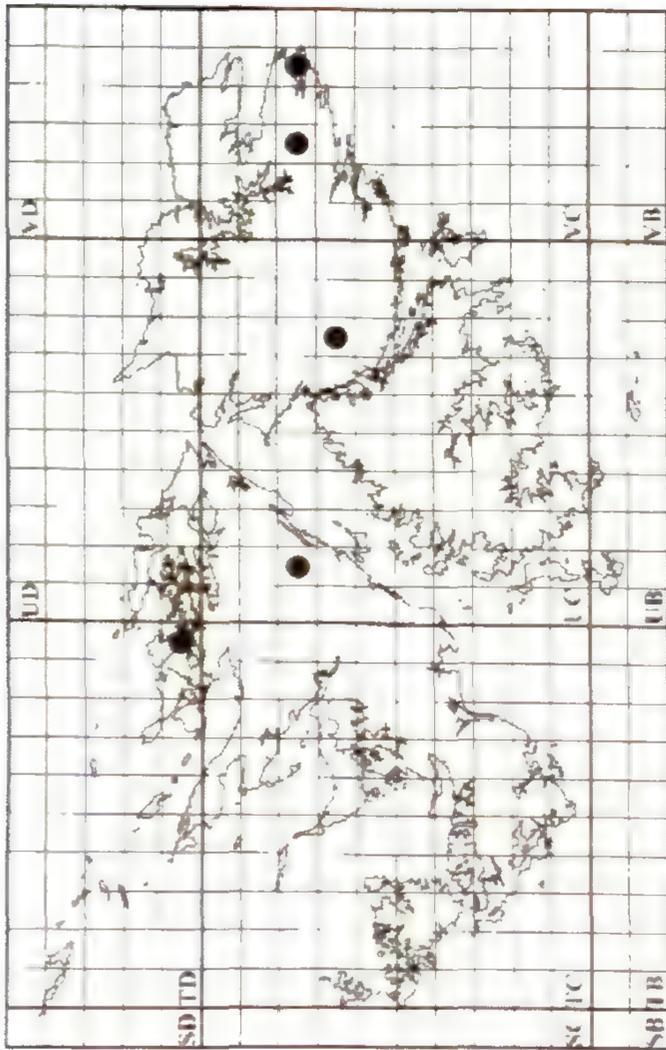


Figure 3. *Huperzia fuegiana*

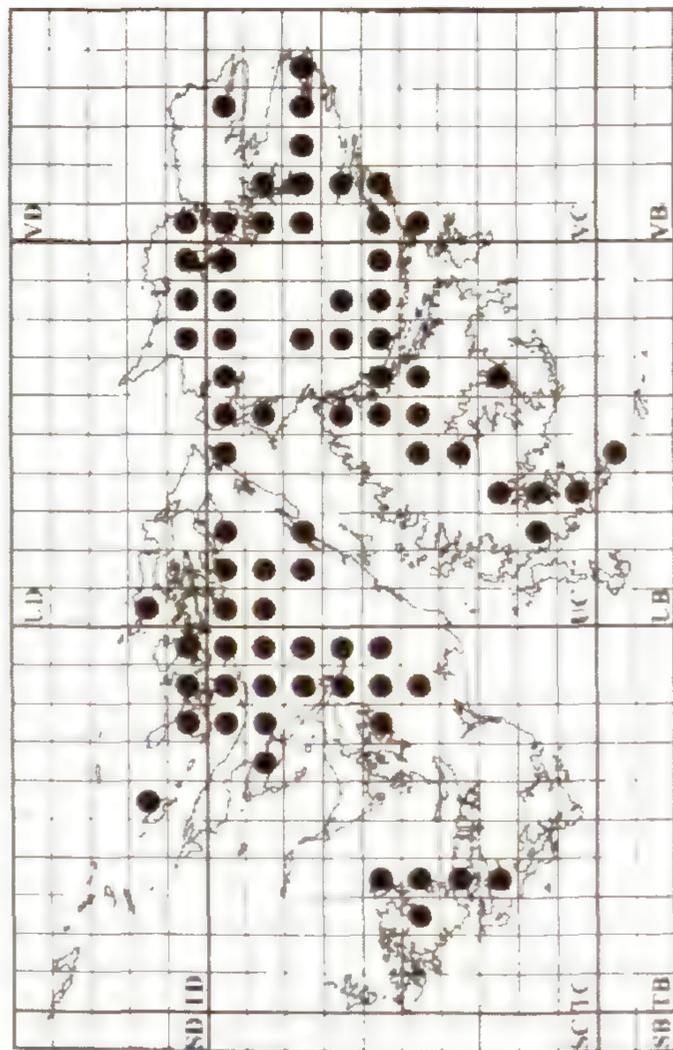


Figure 5. *Lycopodium magellanicum*

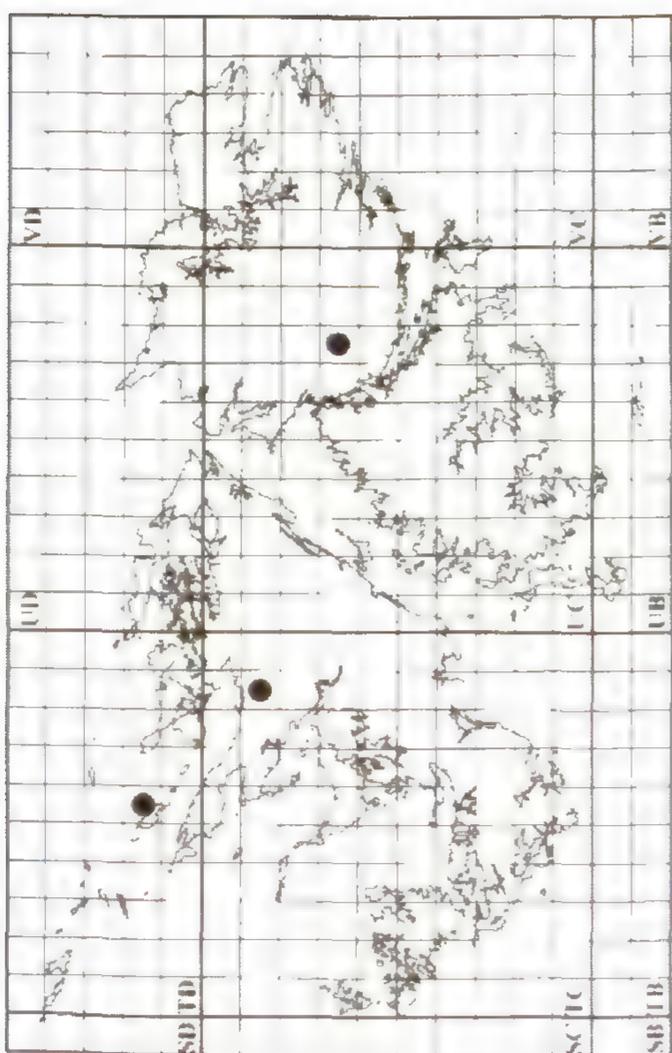


Figure 7. *Asplenium dareoides*

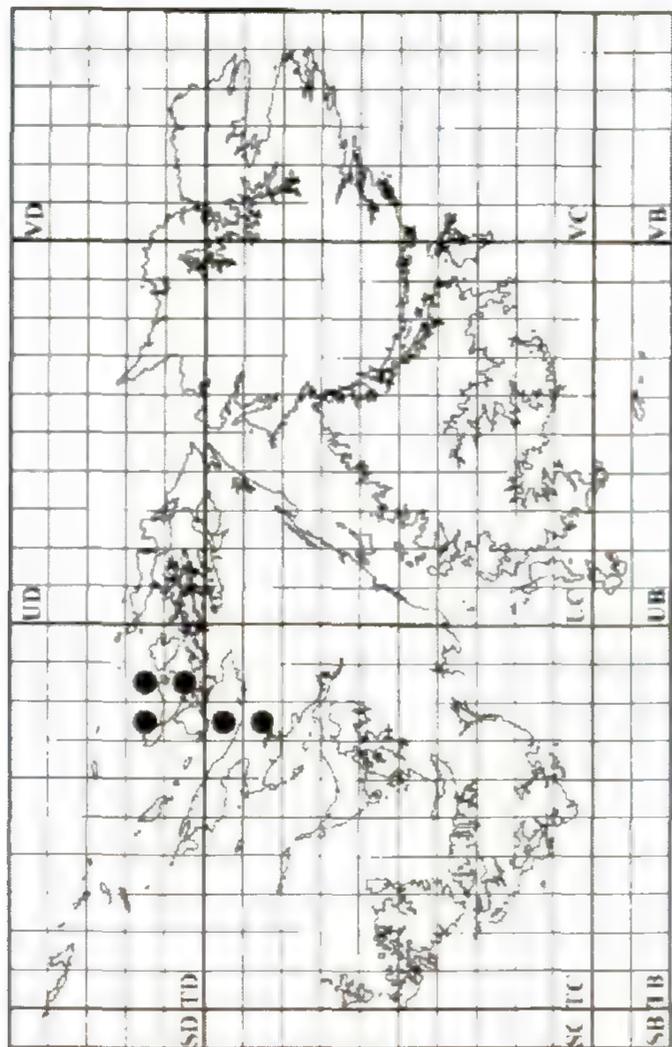


Figure 8. *Blechnum cordatum*

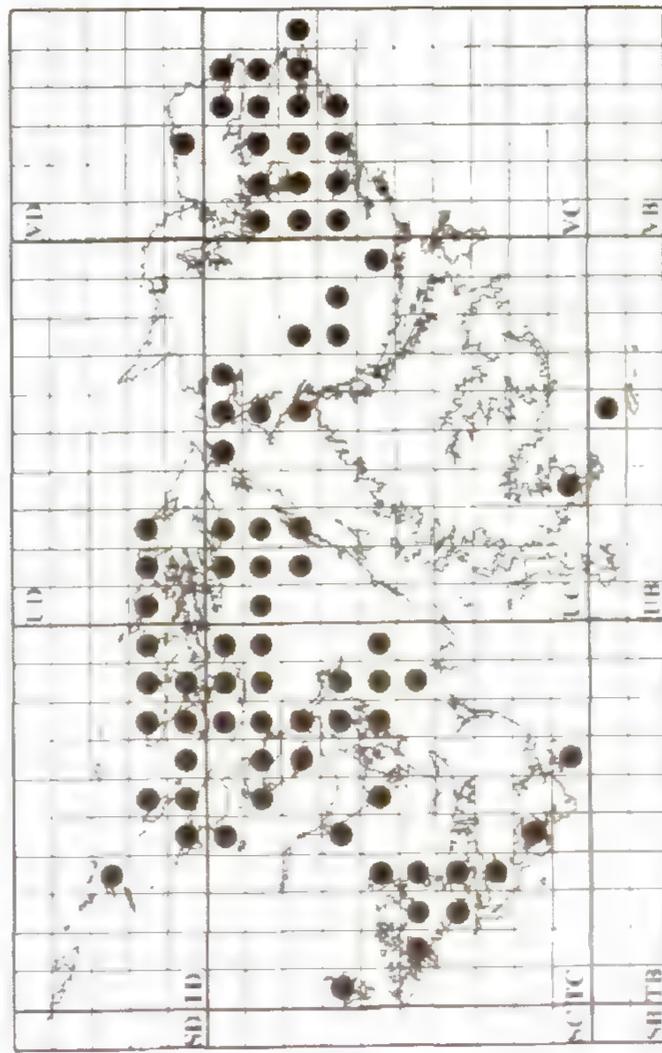


Figure 9. *Blechnum magellanicum*

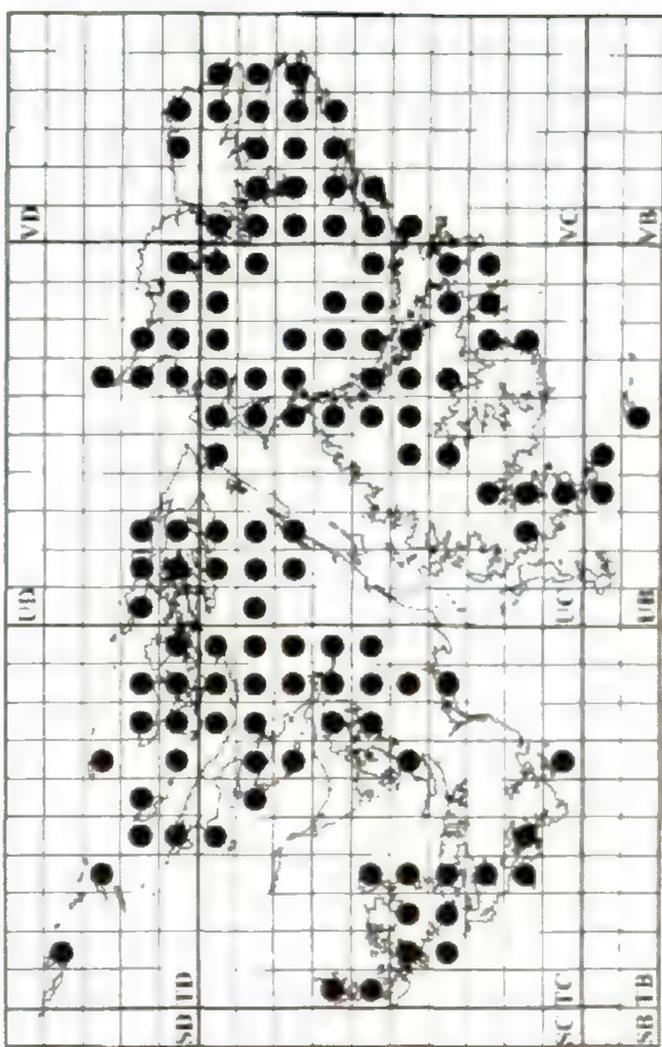


Figure 10. *Blechnum penna-marina*

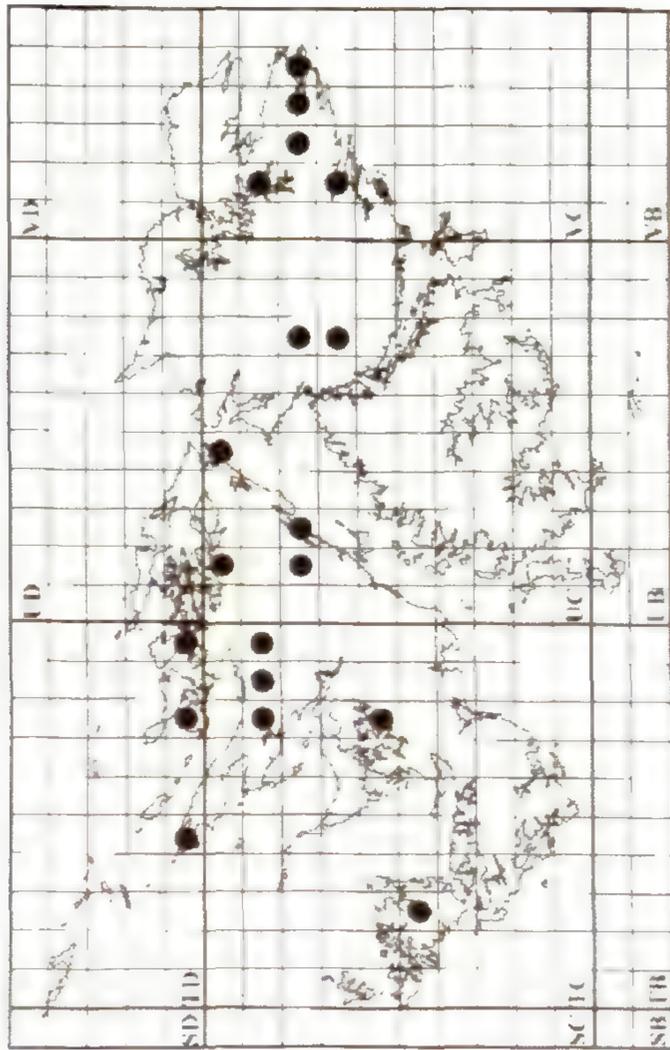


Figure 11. *Polystichum mohrioides*

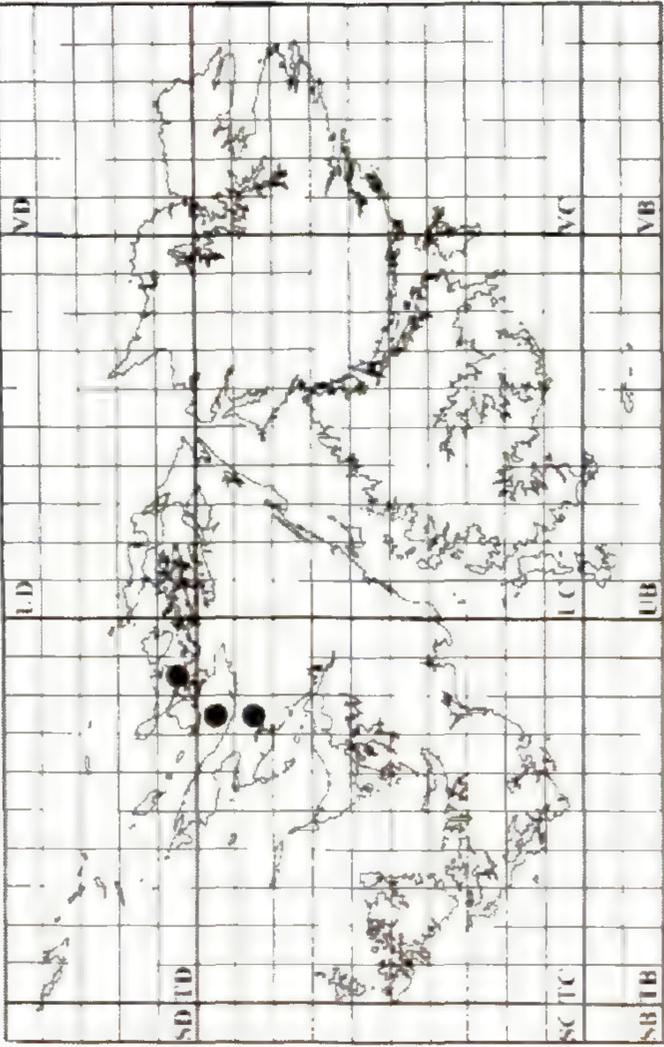


Figure 12. *Rumohra adiantiformis*

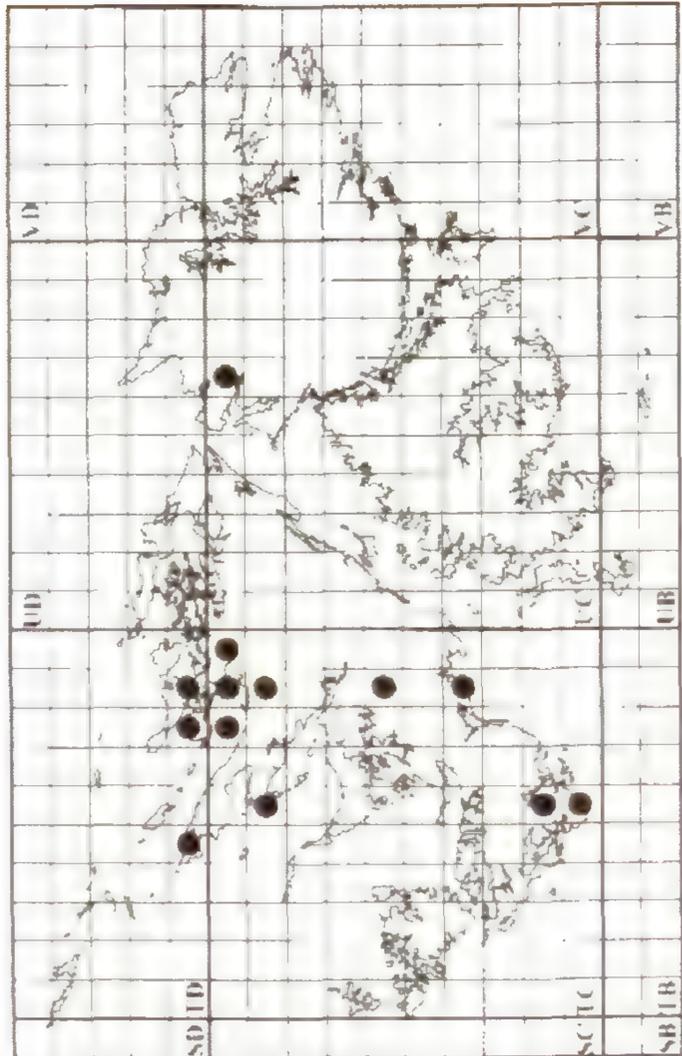


Figure 13. *Gleichenia cryptocarpa*

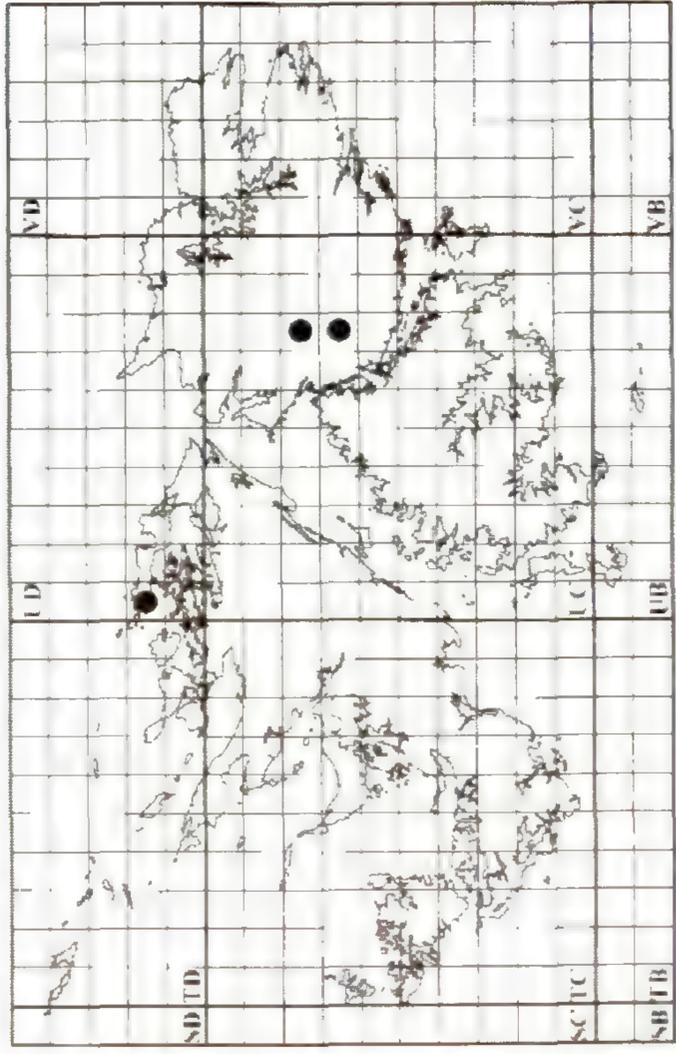


Figure 14. *Grammitis poeppigiana*

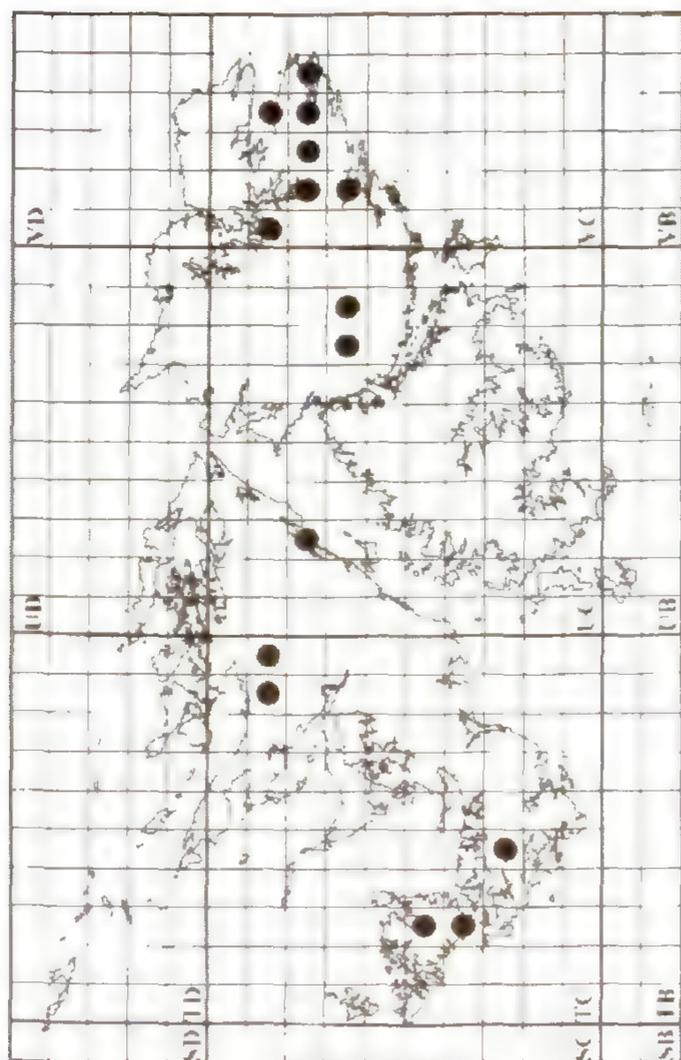


Figure 15. *Hymenophyllum caespitosum*

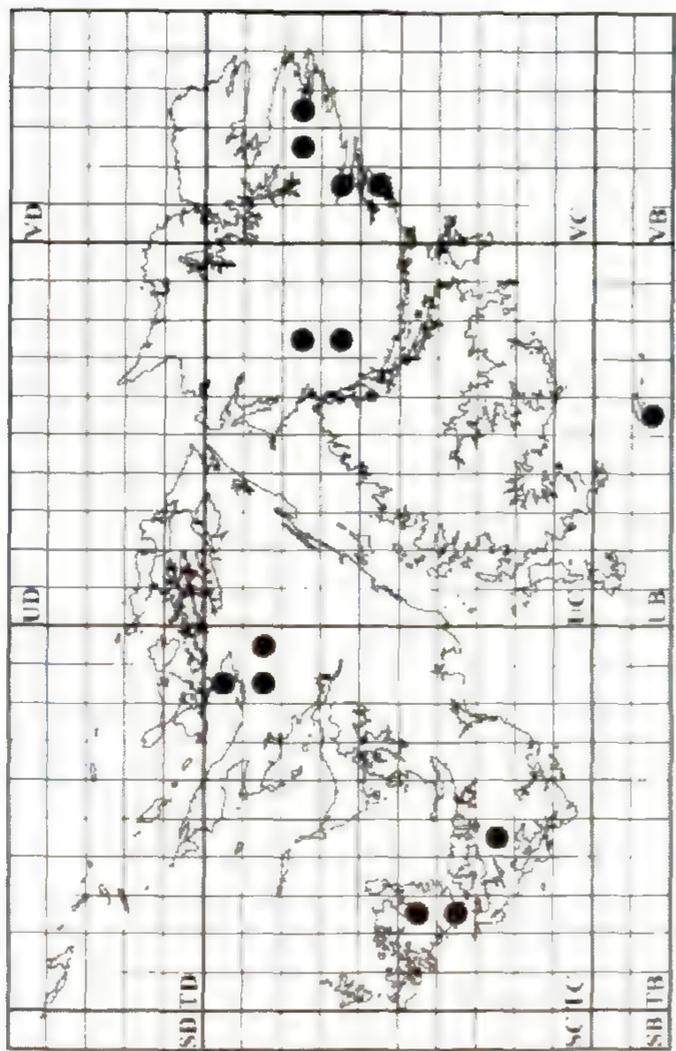


Figure 16. *Hymenophyllum falklandicum*

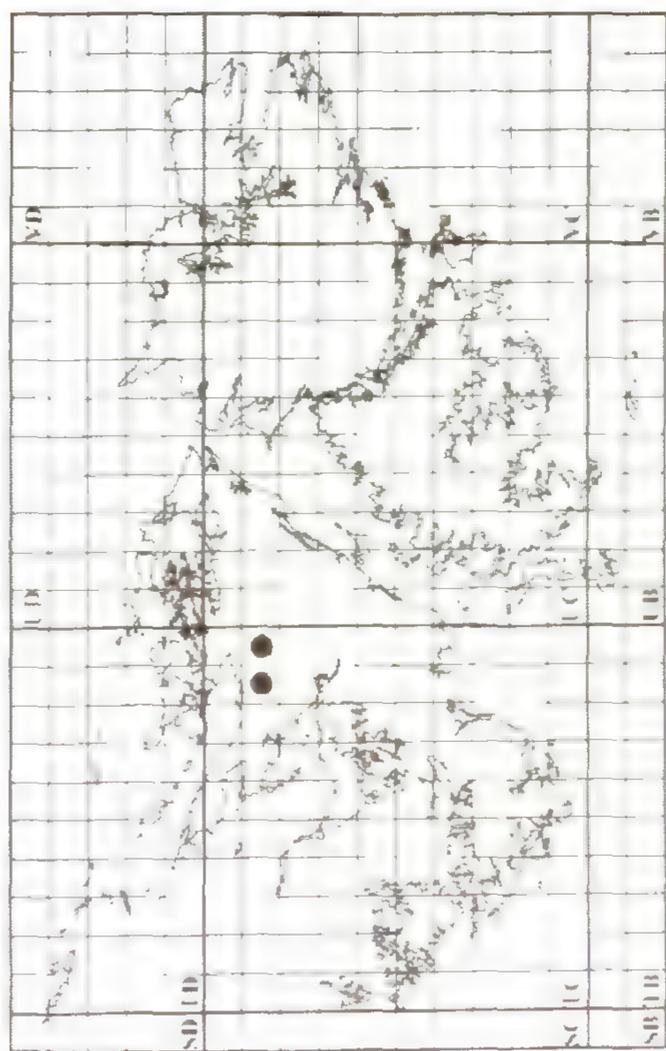


Figure 17. *Hymenophyllum tortuosum*

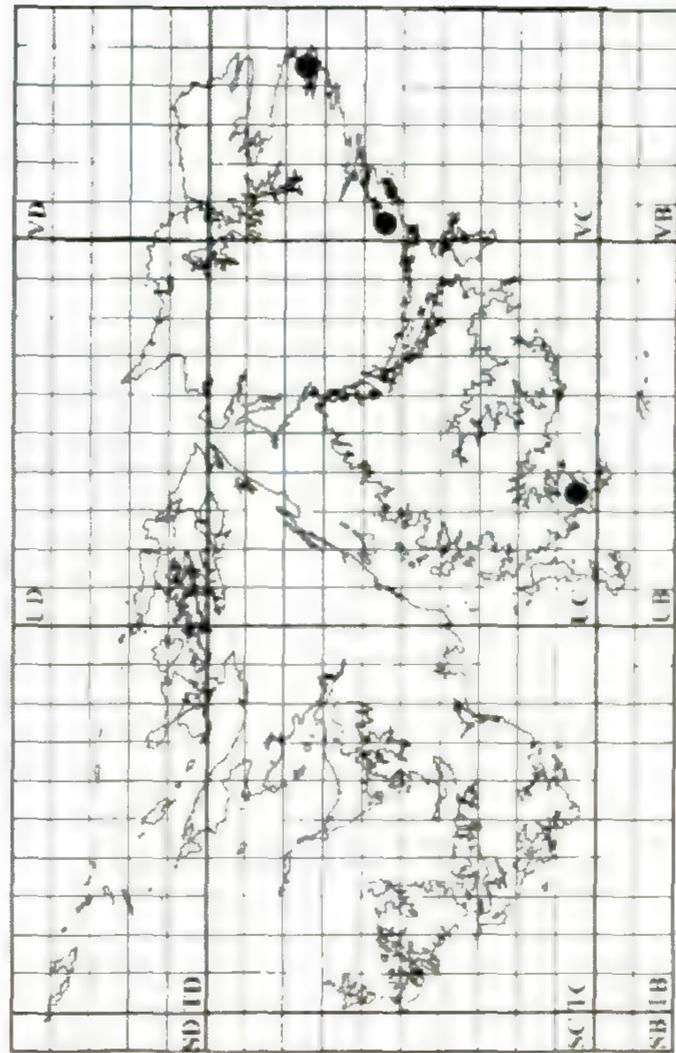


Figure 18. *Botrychium dusenii*

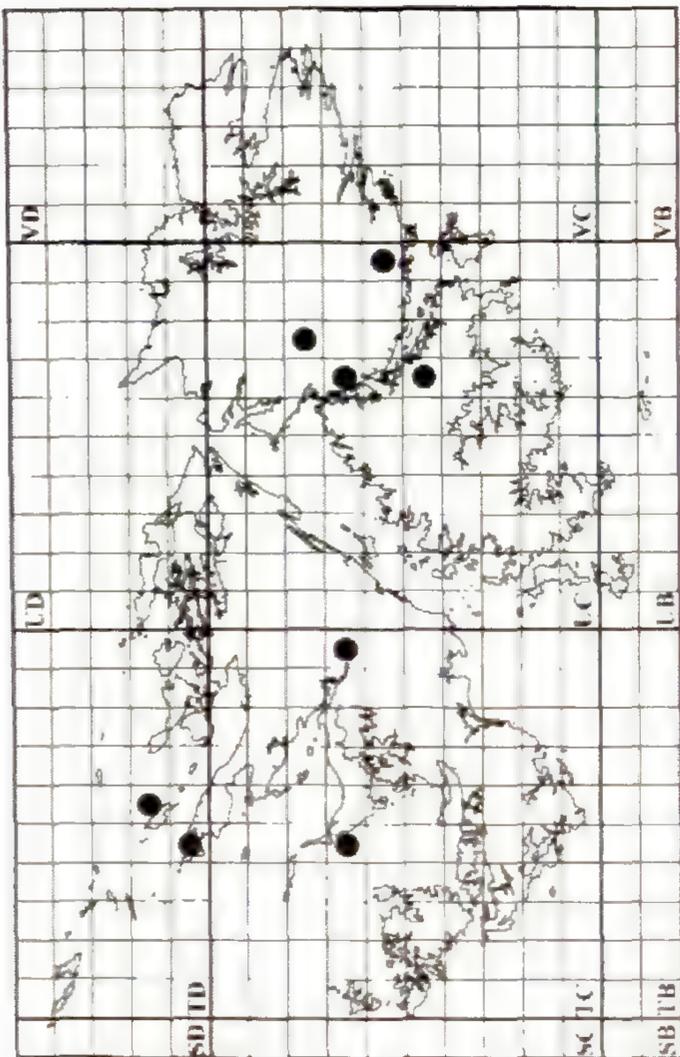


Figure 20. *Cystopteris fragilis*

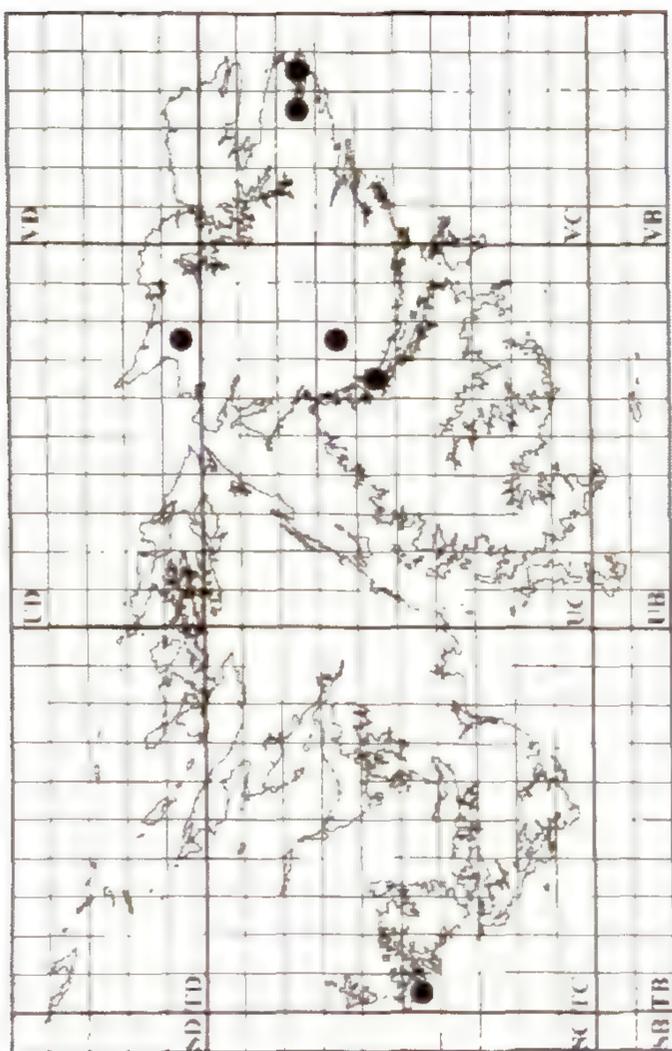


Figure 19. *Ophioglossum crotalophoroides*

**THE IMPORTANCE OF RECENT POPULATION HISTORY FOR  
UNDERSTANDING GENETIC DIVERSITY IN THREATENED  
SPECIES, WITH SPECIAL REFERENCE TO  
*DRYOPTERIS CRISTATA***

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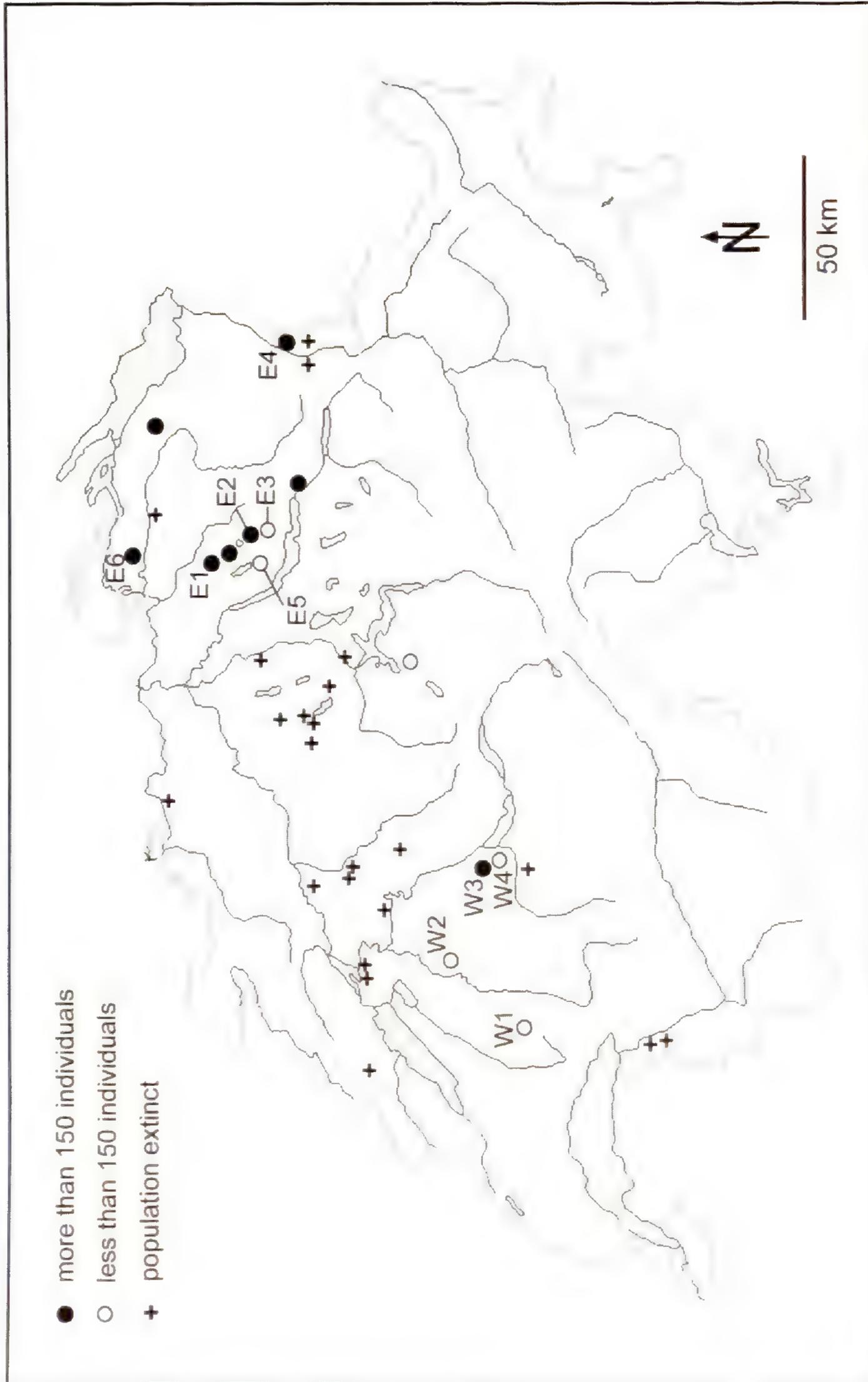
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Key words: *Dryopteris cristata*, conservation, genetic bottleneck, genetic drift, genetic variation, population history, population size, spatial genetic substructure.

**ABSTRACT**

The maintenance of genetic diversity and stochastic losses of diversity during periods of small population size have become major points of concern in conservation biology. However, empirical research on random evolutionary processes in natural plant populations is still scarce and is reviewed here in comparison to our case study on *Dryopteris cristata*. Detailed recent population histories of this wetland fern have been documented in Switzerland. We found that the lack of correlation between present-day genetic diversity and current population size in this fern, as well as in other newly rare and endangered plant species, is best explained by recent population histories.

Genetic diversity is strongly affected by genetic bottlenecks, which resulted in a loss of about 40% of genetic variation even in the long-lived allotetraploids *D. cristata* and a Hawaiian silversword. In contrast, distinct reductions in population size did not severely reduce genetic diversity in populations of the latter two species in the short-term. Accordingly, there was almost no spatial genetic substructure in populations of *D. cristata*. However, evidence for genetic drift was found in small populations of *D. cristata* and has also been reported for flowering plant species, indicating that small populations are nevertheless prone to random losses of genetic diversity in the long-term. This short review elucidates the importance of recent population history for both population genetics and conservation biology. Understanding population history can substantially improve predictions on the genetic diversity in remnant populations of threatened species. Further studies on natural populations of plant species with different life cycles and ploidy levels remain valuable.



**Map 1.** Present and former distribution of *Dryopteris cristata* in Liechtenstein and Switzerland (Landergott *et al.*, 2000), with location of the ten populations included in the analysis of genetic diversity (population abbreviations see Table 1).

**TABLE 1.** Location and abbreviation of the ten genetically studied Swiss populations of *Dryopteris cristata* with historical population sizes and census number in 1999, category of population history, molecular variance and Mantel test for the correlation ( $r$ ) and its significance ( $P$ ) between spatial distances and genetic distances among 20 individuals per population.

Population abbreviation	Location	Population size <sup>1</sup>				1999	Population history <sup>2</sup>	Molecular variance	Mantel test	
		1881-1945	1946-1979	1980-1998	1999				$r$	$P$
W1	Sâles	S	BN (2)	s	60	I	0.134	0.017	0.400	
W2	Düdingen	L	s	S	60	II	0.534	0.081	0.081	
W3	Schmittmoos	—	—	—	>500	—	0.355	0.013	0.431	
W4	Reutigen	L	s	s	110	II	0.734	0.021	0.341	
E1	Wildert	—	S	I	>500	III	0.311	0.108	0.128	
E2	Robenhuserriet	S	L	L	>500	III	0.384	-0.083	0.260	
E3	Ambitzgi	BN (20)	s	s	130	I	0.197	0.326	0.007	
E4	Ruggellerriet	L	L	L	300-500	—	0.311	0.099	0.125	
E5	Greifensee	—	BN (3)	BN (3)	60	I	0.134	-0.061	0.343	
E6	Barchetsee	—	BN	BN	250	I	0.218	-0.139	0.121	

<sup>1</sup>Population size classes according to Landergott *et al.* (2000): BN = bottleneck of less than 25 individuals (exact records are given in parentheses if available); S = small population with less than 150 individuals; L = large population with more than 150 individuals; lower case letters represent estimates, which were deduced from general remarks on habitat conditions without relying on direct records of *D. cristata*.

<sup>2</sup>Types of recent population history: I = with a historical bottleneck; II = reduction of a formerly large population to a small one before 1945; III = increase of a formerly small population to a currently large one.

## INTRODUCTION

Genetic differentiation can be the result of local adaptation, genetic variation may be correlated with fitness, and genetic diversity is a prerequisite for future selection and adaptation (Booy *et al.*, 2000). The maintenance of genetic diversity has consequently become a central focus of concern in conservation biology (Ellstrand & Elam, 1993). Resources for conservation efforts are limited, and accurate predictions regarding the genetic diversity in populations of threatened species are needed. In this context, the stochastic loss of genetic diversity during periods of small population size is an important factor (Barrett & Kohn, 1991). Genetic diversity has been found to be positively correlated with present-day population size in some plant species (e.g. Ellstrand & Elam, 1993; Raijmann *et al.*, 1994; Fischer & Matthies, 1998). However, no such correlation has been reported for several rare and endangered species, and this outcome has often been suggested to be due to assumed changes of population size in recent population history (Ellstrand & Elam, 1993; Kull & Paaver, 1997; Kahmen & Poschlod, 2000; Lutz *et al.*, 2000; Schmidt & Jensen, 2000; Fréville *et al.*, 2001; Podolsky, 2001). As recent historical population sizes usually remain unknown, empirical research on the effects of genetic bottlenecks and drift on wild plant populations is almost lacking (Booy *et al.*, 2000; but see Richards *et al.*, 2003).

The stochastic loss of genetic diversity (specifically, allelic richness) associated with a bottleneck has been studied in artificially founded populations of *Sarracenia purpurea* (Schwaegerle & Schaal, 1979), the Hawaiian Mauna Kea silversword, *Argyroxiphium sandwicense* ssp. *sandwicense* (Friar *et al.*, 2000) and *Rutidosia leptorrhynchoides* (Young & Murray, 2000). A distinct founder effect has also been reported for a population of *Cypripedium calceolus*, which existed for presumably no more than 200 years (Kull & Paaver, 1997), and for a single-founder population of *Trifolium amoenum* (Knapp & Connors, 1999). Accordingly, out of 13 studied populations of the locally rare *Pedicularis palustris*, lowest genetic variation has been reported for a nowadays large population of recent origin (Schmidt & Jensen, 2000). By comparing cytoplasmic diversity in a population of *Thymus vulgaris* before and after fire, Manicacci *et al.*, (1996) showed that disturbances may severely reduce genetic diversity. Founder effects may locally cause a shift from nucleo-cytoplasmic to purely cytoplasmic determination of sex and lead to high frequencies of females in colonising populations of the gynodioecious *T. vulgaris* (Manicacci *et al.*, 1996). The stochastic nature of founding events has also been documented in *Silene latifolia* with younger populations displaying higher genetic differentiation than older ones (McCauley *et al.*, 1995). In common species with substantial gene flow among populations, however, genetic diversity can be restored rapidly with time after a founder event (von Flüe *et al.*, 1999; Richards *et al.*, 2003).

In ferns, the relation between population history and genetic diversity has been discussed with respect to the colonisation of patchy rock habitats (Holderegger & Schneller, 1994; Schneller & Holderegger, 1996a; Vogel *et al.*, 1999). Genetic diversity has been found to be positively correlated with population age in *Asplenium ruta-muraria*, indicating initial single spore colonisation and subsequent multiple colonisation events with increasing population age (Schneller & Holderegger, 1996a).

Another opportunity for studying effects of recent population history on present-day genetic diversity is offered by the population dynamics of threatened species caused by man-made habitat disturbances. For the locally rare and endangered wetland fern *Dryopteris cristata*, recent population histories in Switzerland could be reconstructed

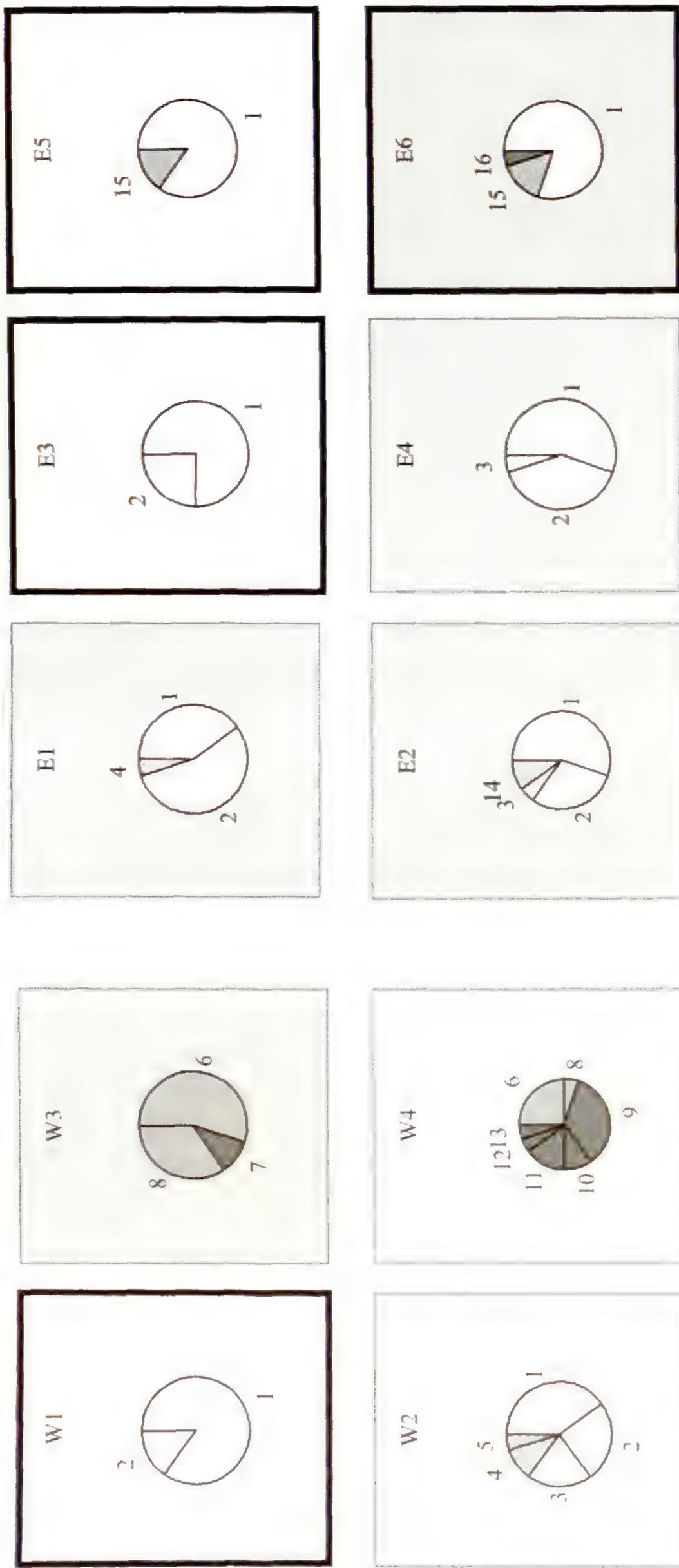
(Lander Gott *et al.*, 2000) and present-day genetic diversity assessed (Lander Gott *et al.*, 2001). Here, additional data are presented on the spatial genetic structure within populations of *D. cristata*. Our aim is to evaluate, illustrate and discuss the results of this case study from the perspective of conservation biology. We discuss implications for conservation in general by including comparable, but scarce, empirical studies on the influence of recent population history on present-day genetic diversity in newly rare and endangered plant species.

### **DRYOPTERIS CRISTATA-SPECIFIC BACKGROUND**

The Crested Buckler fern, *D. cristata* (L.) A. Gray, has become rare and endangered in southwestern Central Europe (references in Lander Gott *et al.*, 2000). In Switzerland, at the southern border of the species' European distribution, 22 (62% of all described) populations are extinct due to habitat destruction, and only 14 populations remained in 1999 (Map 1; Lander Gott *et al.*, 2000). The habitats of the surviving populations are best characterised as different remnants of formerly exploited, but not totally destroyed peat bogs. The commercial exploitation of peat bogs until approximately 1945 and their subsequent management as conservation areas caused substantial changes in population sizes of *D. cristata*. In a previous study, we reconstructed fluctuations in most of the Swiss populations of *D. cristata* over 120 years using herbaria and literature data (Lander Gott *et al.*, 2000). However, even for this attractive fern species, and in a study area with a rich floristic tradition, historical records of population sizes remained incomplete (Table 1). By including current population sizes determined in a field survey in 1999, it was nevertheless possible to establish three types of recent population histories: (I) the occurrence of a severe historical bottleneck of less than 25 individuals, (II) the reduction of a formerly large population (more than 300 individuals) to a small remnant (less than 150 individuals) before 1945 and (III) the increase of a formerly small population to a presently large one (Table 1; Lander Gott *et al.*, 2000).

We estimated genetic diversity in 14 populations of *D. cristata* from Switzerland and southern Germany by random amplified polymorphic DNA (RAPDs; Lander Gott *et al.*, 2001). In each of the 14 studied populations, 20 individuals were randomly sampled throughout the population area. This sample size is recognised as sufficient to provide accurate genetic diversity estimates for plant populations (Nybom & Bartish, 2000). RAPD diversity of *D. cristata* was extraordinarily low in the study area (for discussion see Lander Gott *et al.*, 2001). However, the detected genetic variation within populations was not correlated with current population sizes (Figure 1; Table 1). In a hierarchical analysis of molecular variance (AMOVA), 15% of total variance was attributed to variation among three geographic regions (western and eastern Switzerland and southern Germany), 34% to variation among populations within regions, and only 51% to variation within populations. High population differentiation was indicated by a  $F_{ST}$ -value of 0.49 as well, and genetic divergence among populations was not correlated with geographic distances. These findings suggested very limited gene flow among populations of *D. cristata*. The absence of gene flow as an equalising force and the assumed selective neutrality of RAPD markers allowed us to investigate the effects of random evolutionary processes in recent population history on the genetic diversity in natural populations of *D. cristata*. Note that the categorisation of population size was deduced from the distribution of census numbers found in the studied populations (Lander Gott *et al.*, 2000). Population size classes (Table 1) are thus somewhat arbitrary, and critical population sizes are likely to be different for other plant species with

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**Figure 1.** Frequencies and distribution of 16 RAPD multi-band phenotypes in the ten studied populations of *Dryopteris cristata* from western and eastern Switzerland according to Landergott *et al.*, (2001). RAPD phenotypes No. 1, 2, 3, 5 and 14 were found in southern Germany as well (data not shown). White phenotypes occurred in all three geographical regions, hatched phenotypes occurred in two regions, faint grey phenotypes were restricted to single regions and dark grey phenotypes were restricted to single populations. Large populations with more than 150 individuals are underlined with a grey background, and populations with recent historical bottlenecks of less than 25 individuals are marked with bold border lines (population abbreviations see Table 1).

different life histories and ploidy levels. As no information was available on historical population sizes of *D. cristata* from southern Germany (Lander Gott *et al.*, 2001), the following considerations will focus on the ten Swiss populations included in the RAPD analysis (Map 1; Table 1).

### THE PAST EXPLAINS THE PRESENT

In conservation biology, the number of multi-locus genotypes present in a population has been supposed to be a more important measurement of genetic diversity than the number of single variable markers (Schneller & Holderegger, 1996b). Molecular variance (Table 1) is based on genetic distances among RAPD multi-band phenotypes and on their numbers and frequencies (Excoffier *et al.*, 1992; Fischer & Matthies, 1998), which are visualised for the ten study populations of *D. cristata* in Figure 1.

Present-day RAPD diversity in populations of *D. cristata* was most prominently affected by recent historical genetic bottlenecks (population history type I; Table 1). In populations E3 and W1, severe bottlenecks were caused by peat exploitation. Only 20 individuals survived in population E3 in 1892, at the same place where we found 130 individuals in 1999 (Table 1; Lander Gott *et al.*, 2000). At Sâles (population W1), *D. cristata* was considered to be abundant in 1905, but only a small population was reported in 1929, which then has been argued to become extinct due to further habitat destruction in the near future. By 1959, only two remnant individuals were reported from there, but in 1999 we found again 60 individuals at Sâles (Lander Gott *et al.*, 2000). In contrast, genetic bottlenecks in populations E5 and E6 were most probably due to the recent establishment of new populations by a few founder individuals (Table 1). This could be inferred from the fact that both localities were thoroughly investigated before *D. cristata* had been reported there for the first time (Lander Gott *et al.*, 2000). All four populations with recent bottlenecks were characterised by significantly decreased genetic variation, as compared to populations without bottlenecks (Table 1; *U*-test,  $P < 0.02$ ; Lander Gott *et al.*, 2001). Furthermore, the dominance of a widespread RAPD multi-band phenotype was a common feature of these recently bottlenecked populations of *D. cristata* (frequency of phenotype No. 1  $\geq 0.75$  in all four cases; Figure 1). They comprised less rare RAPD phenotypes than most of the other studied populations (Lander Gott *et al.*, 2001). The stochastic loss of genetic diversity during severe bottlenecks has been predicted by population genetic theory for diploid, outbreeding organisms (e.g. Barrett & Kohn, 1991). For polyploid species, however, less of an effect of a bottleneck on the genetic diversity would be expected, because high levels of segregational heterozygosity could nevertheless be maintained within populations (Barrett & Kohn, 1991; Bretagnolle *et al.*, 1998). In contrast, the four recently bottlenecked populations of the allotetraploid fern *D. cristata* ( $2n = 164$ ) showed a substantial loss of genetic variation (reduction in molecular variance = 40%; Table 1) as compared to populations without bottlenecks. A similar loss of genetic diversity, as measured by the number of microsatellite alleles within population (reduction = 36%) and the proportion of polymorphic loci (reduction = 43%) has been reported in the allotetraploid Mauna Kea silversword *A. sandwicense* ssp. *sandwicense* after a genetic bottleneck of two individuals, which was associated with the populations re-introduction (Friar *et al.*, 2000).

In *D. cristata* from Switzerland, highest genetic variation was found in two currently small populations W2 and W4 (molecular variances = 0.534 and 0.734, respectively; Figure 1; Table 1). These populations were large ones at the beginning of

the 20th century, but subsequently suffered a severe reduction in population size due to peat exploitation, leaving as few as 50 to 150 individuals of *D. cristata* in small marginal habitats by 1945 (population history type II; Table 1; Landergott *et al.*, 2000). Similar genetic variation was detected in a putatively old large population from southern Germany (B4, molecular variance = 0.655; Landergott *et al.*, 2001). Unfortunately, there were no populations documented to have always been large during the past 120 years, except for the geographically isolated population E4 (Landergott *et al.*, 2001). However, the comparatively high molecular variance still maintained in the small populations W2 and W4 of *D. cristata* suggested that a distinct reduction in population size to less than 150 individuals did not substantially reduce genetic variation in populations of this long-lived, homosporous fern species in the short term. Similarly, a reduction in size to fewer than 50 plants in the remnant natural population of the long-lived Mauna Kea silversword was not accompanied by a significant loss of genetic diversity (Friar *et al.*, 2000). High genetic variation was also maintained in large and small remnants of formerly large metapopulation systems of *Cyrtopodium calceolus* (Kull & Paaver, 1997) and *Pedicularis palustris* (Schmidt & Jensen, 2000) and in fragmented subpopulations of *Haplostachys haplostachya* (Morden & Loeffler, 1999). In *Clarkia dudleyana*, a historically large but currently small population exhibited still high genetic variation, and classifying this population as either a small or large one has been reported to alter several trends of correlations between population size and various measures of genetic diversity (Podolsky, 2001).

A prerequisite for the maintenance of a considerable amount of genetic diversity in small population-remains is the random distribution of genotypes within populations. For several predominantly outcrossing seed plants, weak spatial genetic structuring within populations has been reported (Heywood, 1991). Even less spatial genetic substructure would be expected in populations of long-lived, homosporous ferns, due to their high spore production and great potential for long-distance spore dispersal (Cousens, 1988). To get some insights into the spatial genetic structure within populations of *D. cristata*, we performed Mantel tests based on the spatial distances and the squared Euclidean genetic distances among the 20 RAPD phenotypes for each of the 14 studied populations separately (with 999 permutations using NTSYS-pc; Rohlf, 1998). A significant positive correlation was found only in the recently bottlenecked population E3 (Table 1; data of four German populations not shown). Because of the small sample size per population and because Mantel tests do not have high resolving power to detect spatial genetic structure within populations (Heywood, 1991), results should be interpreted with caution. However, at a larger spatial scale, they corroborate the proposed maintenance of considerable genetic variation in small remnants of formerly large populations of *D. cristata*. Furthermore, in small populations where a larger proportion of individuals has been sampled, they indicate little or no spatial genetic structure at the small scale. In contrast, positive autocorrelations have been observed at the small spatial scale in some populations of the rock fern species *Pteris multifida* (Murakami *et al.*, 1997) and *Asplenium trichomanes* subsp. *quadrivalens* (Suter *et al.*, 2000). Further studies of spatial genetic structure and its relation to breeding systems in natural populations are needed for general predictions on the maintenance of genetic variation in small population-remains of ferns, but also in flowering plants (Stehlik & Holderegger, 2000).

Despite the comparably high level of genetic variation maintained in some small populations of *D. cristata*, these populations could be prone to future stochastic losses

of genetic variation through random genetic drift (Barrett & Kohn, 1991). A theoretical prediction on genetic drift states that allele frequencies within populations fluctuate and tend to drift apart, while overall average allele frequencies among populations remain constant (Hartl & Clark, 1997). In currently small and/or recently bottlenecked populations, deviations of RAPD marker frequencies within populations from their overall frequencies were in fact significantly increased, compared with marker frequency deviations in large populations (Lander Gott *et al.*, 2001). This gave evidence that small populations of *D. cristata* are actually under genetic drift, which might lead to random loss of alleles in the future. Severe genetic erosion due to drift occurred in the short term in small populations of the short-lived *S. latifolia* when significant gene flow was absent (Richards *et al.*, 2003). Morden and Loeffler (1999) reported a substantial increase in the number of RAPD markers either present or absent in all individuals of the smallest subpopulation of *Haplostachys haplostachya* relative to other subpopulations, suggesting that drift was moving this subpopulation towards fixation of alleles. Kull and Paaver (1997) emphasised remarkable fluctuations of allele frequencies among isolated remnant populations of *Cypripedium calceolus* as well. Further evidence for genetic drift in small natural populations has been observed in *Salvia pratensis* and *Scabiosa columbaria* as judged from substantially higher genetic differentiation among small populations than among large ones (van Treuren *et al.*, 1991). Accordingly, greater genetic differentiation among populations of *Cyclamen balearicum* from habitat islands in southern France than among populations from the true Balearic islands (Affre *et al.*, 1997) has been attributed to genetic drift in small relict populations following habitat fragmentation in southern France in the past 500 years (Thompson, 1999).

Finally, the intermediate level of genetic variation found in two of the largest populations of *D. cristata*, E1 and E2, could also be explained by their shared population history (type III; Table 1). These populations had first been recorded as small ones and substantially increased in size in the second half of the 20th century (Lander Gott *et al.*, 2000), presently showing high viability as indicated by spore production (Lander Gott, personal observation). Hence, ecological factors might be more important for short-term population viability in *D. cristata* than genetic diversity as assessed by neutral markers. Accordingly, viable populations with complete allozyme uniformity have been reported for the inbred, polyploid ferns *Asplenium ruta-muraria*, *A. septentrionale* and *Polypodium vulgare* (Schneller & Holderegger, 1996b). Notice that the relevance of neutral genetic variation for conservation purposes is presently under discussion (Crandall *et al.*, 2000; Fischer *et al.*, 2000; Podolsky, 2001), but in the end, adaptively significant genetic variation will be affected by stochastic losses during periods of small population size in much the same way as neutral variation.

### CONCLUSIONS

As far as *D. cristata* is concerned, its extraordinarily low overall genetic diversity, somehow conflicting with its high genetic population differentiation, hinders straightforward conclusions for the species' conservation. However, this fern is presently stated to be vulnerable (IUCN, 1994) in the region of western Switzerland (Lander Gott *et al.*, 2000) and it is the focus species of a local conservation project at the Botanical Garden of Fribourg in Switzerland (Kozłowski, 1999). Without knowledge of possible adaptive differences among populations, the best strategy maintains genetically distinct populations. For example, in western Switzerland, the RAPD

phenotypes of population W1 are a subset of W2 and, likewise, those of W3 are essentially a subset of W4 (Map 1; Figure 1). Preservation of genetic diversity in this region requires priority conservation of populations W2 and W4 (Figure 1; Table 1). Their small sizes make them prone to genetic drift, however, and *in situ* increases of their population sizes are thus desirable. Unfortunately, the autecology of *D. cristata* is poorly known (Page, 1997). Studies on its breeding system, safe sites, and recruitment of individuals in natural populations would considerably improve conservation strategies for this threatened fern species.

In general, the studies reviewed in this article demonstrate the importance of recent population history for both population genetics and conservation biology. Especially in newly rare, threatened species, substantial recent historical changes in population size should be expected. Therefore, conservation practice requires an understanding of the effects of stochastic forces on genetic diversity (Barrett & Kohn, 1991), and theoretical predictions on random evolutionary processes during periods of small population size need to be tested in natural populations of plant species with different life histories and ploidy levels. Since population history is often incompletely known, the empirical base is still small and further case studies that consider genetic diversity in the light of population history will be most worthwhile. Floristic records in herbaria and in the literature, as well as continuous monitoring of small and large natural populations are important in this regard. If adequate records are available, population history can substantially improve predictions on genetic diversity in remnant populations of threatened species and thereby help in choosing priority populations for conservation.

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