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Lobelia gloria-montis

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A Review of the Genetic and Evolutionary Effects of Plant Invasions

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Invasive species are now recognized as a worldwide problem by threatening global biodiversity (Heywood, 1989; Lonsdale, 1999), contributing to major environmental damage and economic losses (Pimentel et al., 2000), and altering ecosystem structure and function through their impacts on soil nutrient levels (Vitousek and Walker, 1989), altered fire regimes (D'Antonio and Vitousek, 1992), native seedling recruitment (Richardson et al., 1989; Walker and Vitousek, 1991) and reduced stream-flow (van Wilgen et al., 1992; van Wilgen et al., 1996). Mark Williamson (1996) published *Biological Invasions*, a book reviewing current literature that addressed a broad range of issues pertaining to biological invasions of both plants and animals. One chapter of the book dealt with the genetic and evolutionary effects of biological invasions, and focused its review on two main points: 1) genetics may affect the success of invaders, and evolution may occur following invasion; and 2) studies of biological invasions can be used to better understand risks associated with introducing new species and genotypes and in releasing genetically engineered organisms.

Williamson (1996) gives examples of how genetics plays roles in invasions. He states that individual genes or groups of genes could have an effect on invasion success, and points to the differential success of *Impatiens capensis* versus *I. noli-tangere* in England as one such example. He

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indicates that that gene frequencies can also change during the course of an invasion, using the example of rabbits adapting to the myxoma virus. He cautions about over-emphasizing the importance of genetic changes in theorizing about the establishment and success of invasive species without conclusive proof, but recognizes that all introduced invasive species will eventually undergo genetic changes in the long run. The important and more immediate question concerning invasive species and their genetic and evolutionary effects is whether or not identifiable genetic differences exist prior to invasions that contribute to invasion success or whether they occur during an invasion and result in the rapid spread and proliferation of the exotic species. Other possibilities include genetic changes in invasive species over a longer period of time, well after a species has already become established. In addition, the implications of genetically engineered organisms as potential invasive species are discussed and associated concerns are raised. The following sections will address these issues and provide examples from the current body of literature.

Genetic Differences Allowing Invasion

Williamson (1996) uses examples of closely related species of *Impatiens*, sparrows, *Rhizobium* spp., and rats to demonstrate the importance of genetic differences between invaders and non-invaders. In the case of the sparrows and rats, he attributes the differential success of the invaders versus the non-invaders to their greater abundance, wider ranges in their native region and therefore, greater genetic diversity and adaptability to more environments. In contrast, single or a few gene differences contribute to the success of *Rhizobium* invasions on different legume species (Young and Johnston, 1989).

There are many examples in the Hawaiian flora of native genera with non-native congeners that have become established in the islands. Specific examples include the native *Bidens* species (Asteraceae) and the invasive *Bidens pilosa*, and native and non-native species of *Heliotropium* (Boraginaceae), *Chenopodium* (Chenopodiaceae), *Ipomoea* (Convolvulaceae), *Acacia* (Fabaceae), *Abutilon* (Malvaceae), *Boerhavia* (Nyctaginaceae) *Argemone* (Papaveraceae), *Panicum* (Poaceae), and *Rubus* (Rosaceae) among others (Wagner et al., 1990). Obviously, these species are genetically different from one another to various degrees, but whether or not these genetic differences contribute to the abundance and spread of the non-native taxa versus the more localized distribution of most of the native species is unknown. Barrett (1987) demonstrated that genetic diversity was commonly higher in wide ranging invasive

species than related endemic species, and Meekins et al. (2000) hypothesized that the same might be true for the widespread and invasive *Alliaria petiolata* (Brassicaceae) if compared to *A. brachycarpa*, a narrowly distributed species endemic to the Caucasus mountains. Albert et al., (1997) identified genetic differences between the invasive, non-native *Carpobrotus edulis* (Aizoaceae) and the less aggressive, presumed native *C. chilensis* in California, and discuss hybridization between the taxa (discussed in the next section). Lambrinos (2001) looked at the invasion histories of two related non-native species in California, the sexually reproducing *Cortaderia selloana* and the asexually reproducing, agamospermous *C. jubata*. Although similar in morphology and introduced at approximately the same time, *C. selloana*'s invasiveness has increased with time, and it has expanded at twice the rate as the asexual *C. jubata*. Lambrinos (2001) attributes this difference to the ability of the sexual and genetically diverse *C. selloana* to adapt to a greater diversity of landscapes than the asexual *C. jubata*, with its reduced amount of genetic diversity.

The absence of sexual reproduction is not always a detriment to invasions, however, as evidenced by the apomictic African grass *Pennisetum setaceum*, with high phenotypic plasticity, a variable chromosome number ($2n = 18, 27, 54$) and the greatest altitudinal range of any grass species in the Hawaiian Islands (Wagner et al., 1990; Williams et al., 1995). Nevertheless, several examples indicate that the reduced genetic diversity of colonizing species could prevent the expansion of invaders into a wider range of habitats than might otherwise be possible. This was demonstrated by Jain and Martins (1979) in populations of *Trifolium hirtum* invading California, and by Lambrinos (2001) with *Cortaderia jubata*. Radford and Cousens (2000), in comparing the invasive species *Senecio madagascariensis* to the non-invasive *S. lautus* (Asteraceae) in Australia, determined that species performance differences were probably not genetically fixed which was contrary to other findings of this section. Instead, they seem to have responded to environmental differences. They conclude that invasions must be looked at on a case-by-case basis and that the combination of unique plant genotypes and environments prevent general predictions about which species will become invasive.

Nevertheless, several authors have attempted to identify generalizations about the genetics of invasive plants. Bennett et al. (1998) compared DNA amounts in 156 species of weeds in the British Isles with 2685 non-invasive species and found that DNA amounts per genome in weeds were smaller than in other species. They

state that these findings could either imply that selection exists for smaller DNA amounts and genome size in weeds, or that smaller DNA amounts and genome sizes are useful preadaptations for invasive species. Bennett et al. (1998) also found increased levels of polyploidy in 116 weed species compared to 2357 non-invasive species, results that could reflect increased genetic variation in the invaders. Finally, Rejmanek (1996, 1999) and Grotkopp et al. (1998) also point to a small genome size and suggest that it is the result of selection for a reduced generation time that, among other factors, could contribute to a plant's invasiveness.

Genetic Changes During Invasion

Some species appear to demonstrate a lag time after colonization before they become invasive. Williamson (1996) states that, without common garden experiments, it is not possible to know if a plant's change in invasiveness after a lag period is due to a modification in habitat, or if some genetic change triggered the invasion. He questions whether evidence exists for genetic changes that promote invasions, and states that hybridization events, resulting in invasions or genetic pollution of native species, provide the only concrete evidence of such genetic changes. Other authors (Sun, 1997; Crooks and Soule, 1999) state that the lag times sometimes witnessed could be due to a genetic lag or period in which population numbers are too low. They believe that both a greater number of introductions in the future, or individuals with outbreeding systems, can overcome this lag more rapidly by providing an infusion of new alleles or genotypes. In one example, Dietz et al. (1999) state that anthropogenic disturbance contributes to greater gene flow between populations of the invasive *Bunias orientalis* (Brassicaceae), and that this increase in genetic diversity has made this species more adaptable to a broader range of changing habitats associated with such disturbance regimes. They suggest that further research should explore whether greater genetic diversity of founder populations results in greater plant fitness later in the invasion process. Morrison and Molofsky (1998) address this issue by examining different genotypes of the invasive grass *Phalaris arundinacea*, and conclude, "high levels of genetic diversity increase the likelihood that a particular genotype will flourish and spread into new areas."

Williamson (1996), as previously stated, points to hybridization events as more concrete evidence for genetic changes leading to invasions and the genetic consequences of such invasions. He and other authors (Thompson, 1991; Ellstrand and Schierenbeck, 2000)

use the example from England of *Spartina anglica* (Poaceae), an allotetraploid hybrid between the native *S. maritima* and the North American *S. alterniflora*. The hybrid is more common and vigorous than native *Spartina* species in England, Scotland and Ireland, where it grows in crop-like monotypic stands. Albert et al. (1997) and Gallagher et al. (1997) use morphological and allozyme evidence to demonstrate hybridization between the invasive *Carpobrotus edulis* (Aizoaceae) and the presumably native *C. chilensis* in California. They state that *C. edulis* "is the more likely recipient of introgressed genes than *C. chilensis*" and that the ecological attributes of the hybrids are more similar to *C. edulis*. Because both the invader and the hybrid tend to dominate native communities to different degrees (Weber and D'Antonio, 1999), one of the implications of these hybridization events is that introgression could be developing a novel genotype with greater potential to invade and modify ecosystems, and could also result in genetic assimilation of the native species.

Ellstrand and Schierenbeck (2000) discuss the development of novel genotypes, as well as increased genetic variation, fixed heterosis and the dumping or elimination of genetic load as possible reasons why hybridization events could lead to more vigorous, and therefore, more invasive weeds. They proceed to give 28 such examples of hybridization events resulting in the development of invasive taxa or invasive lineages. They further address the concept that "hybridization" between different or distant populations of the same species may act in the same way as hybridization between different taxa, resulting in more fit offspring better able to invade a wider range of habitats. Barrett and Husband (1990) also mention this as a factor leading to the greater genetic diversity and invasiveness of *Echium plantagineum*, a noxious weed in Australia that resulted from gene flow (i.e., "hybridization") between multiple introduced populations.

Of further concern is the possibility that hybridization among congeners may lead to genetic assimilation or "pollution" of native species (Williamson, 1996). Huxel (1999) claims that invaders may "genetically swamp" native species through increased pollen production or increased fertility, and that this in turn can lead to rapid replacement of the native species by the invader and hybrid populations. Manchester and Bullock (2000) also mention these consequences in discussions on hybridization. Gallagher et al. (1997) state that hybridization between native and non-native *Carpobrotus* species "threaten the genetic integrity of the native species." Further examples of hybridization between native and

non-native taxa, implying possible assimilation of the native, are given by Daehler and Strong (1997a) and Anttila et al. (1998) for crosses between the introduced *Spartina alterniflora* and the native *S. foliosa* in California. Examples from Hawai'i are given by Randell (2000) between the native *Rubus hawaiensis* and the introduced *R. rosifolius* as well as by Wagner et al. (1990) between the native poppy *Argemone glauca* and the introduced *A. mexicana*. The consequences of these hybridization events are yet to be determined. Nevertheless, this issue is another cause for concern when dealing with conservation and protection of Hawai'i's rare flora, especially when considering the number of native taxa with non-native congeners currently established in the Hawaiian Islands, as well as with the continuous introduction of new taxa by the agricultural and horticultural industries. Perhaps, because of this potential for hybridization, particular attention should be paid to non-native plant taxa with native congeners in development of screening systems for the Hawaiian Islands as well as for other regions of the world.

In contrast to all of the preceding examples, Williams et al. (2000) assessed the genetic risks of introducing new non-native plant taxa into New Zealand and concluded that "genetic pollution" of native taxa was only a minimal threat. As more research is conducted, and global commerce further accelerates the movement of, and contact between, previously isolated congeneric taxa, more examples and consequences of hybridization will undoubtedly be discovered.

Genetic and Evolutionary Changes After Invasion

Williamson (1996) states that although invasions occur quickly, the evolution of the invader is slow and may be undetectable for a long period of time. He further claims that significant ecological changes following invasions are the exception rather than the rule. Williamson and Fitter (1996) mention the speculative case of *Epilobium angustifolium*, a species that changed from a rare native to a widespread invader early in the century, but admit that genetic evidence is lacking.

Blossey and Notzold (1995) proposed the "evolution of increased competitive ability" hypothesis to explain the phenomenon that alien species are often larger and produce more seeds in their introduced versus their native range, as observed by Crawley (1987). This hypothesis states that, in the absence of herbivores, selection favors genotypes that have quicker growth rates, greater seed production, larger leaves, or other competitive abilities over genotypes that devote energy and re-

sources to defense against herbivores. They use the example of *Lythrum salicaria*, an invasive plant in North America that, in common garden studies, has higher growth rates and produces more biomass than plants from the native range of Switzerland.

However, most studies that address the hypothesis of increased competitive ability do not support it. Willis et al. (1999) tried to corroborate the hypothesis by investigating whether introduced *L. salicaria* plants were more susceptible to herbivores as a result of this shift in resources, but found little evidence to support the conclusions of Blossey and Notzold (1995). Willis et al. (2000) examined differences between four weeds present in Australia and New Zealand and from their native ranges, and similarly found little evidence that increased plant size is genetically determined. Daehler and Strong (1997b) did find reduced herbivore resistance in introduced *Spartina alterniflora* populations, but state that this could be due to founder effects or herbivore preference rather than evolution of competitiveness in growth. In fact, they actually found that plants with the more rapid growth rates had greater herbivore resistance, in contrast to the findings of Blossey and Notzold (1995). In yet another study, Thebaud and Simberloff (2001) looked at non-native plant species introduced from California and the Carolinas into Europe, and European species introduced into California and the Carolinas, and again found no tendency for the plants to be larger in the non-native regions. They suggest that, when introduced taxa are larger, it may be due to the absence of herbivores from their native ranges, but that each species must be looked at on a case-by-case basis. The underlying conclusion, reiterated by many other authors, is that generalizations about invasive species are difficult to support.

In one example that does suggest genetic changes occurring during and after invasions, Lambrinos (2001) found that populations of *Cortaderia selloana* have changed morphologically over the past 80 years and believe this is because of genetic adjustments since their introduction into California. Innumerable examples exist of invasive plant species in the Hawaiian Islands whose success is frequently attributed to some form of ecological release from their co-evolved herbivores, pathogens and other competitive elements. This presumption is often the driving force behind the search for biocontrol agents of some of the more aggressive and serious invaders. Whether invasive success is due to phenotypic changes as a result of ecological release, the "evolution of (an) increased competitive ability," some combination of the two, or neither should be examined for each spe-

cies, and such assumptions thoroughly tested as part of the investigation into biocontrol. Further research examining differences between introduced plants in their native and non-native ranges throughout the world will likely shed more light on this concept of genetic changes occurring after invasions.

Genetically Engineered Plants

Williamson (1996) addresses the concerns associated with the release of genetically engineered plants and states that invasions often result when a plant finds itself in a new environment. He concludes that since all environments are essentially new to a genetically engineered plant, extreme caution must be taken when releasing them into the environment. He also warns that since genetically engineered plants are generally commercial products, there is an increased likelihood that they will be widely distributed and essentially uncontrollable if they do start to escape from cultivation. Other authors point to several cases of engineered genes spreading from crop plants into wild populations (Klinger and Ellstrand, 1994, Bergelson et al., 1998), and suggest that engineered genes in crops may spread more than wild genes in certain weeds (Bergelson, 1994; Bergelson et al., 1998). Warwick et al. (1999) suggest that genetically engineered plants can change weed communities and populations by escape and invasion of the genetically engineered plants themselves, by hybridization with and selective introgression of engineered genes into weeds or wild plants, and by genetic changes in unrelated populations of plant species resulting from environmental changes, such as the development of herbicide resistant crops and/or weeds. For these reasons, and because of the level of unpredictability of weed invasions in general, several authors (Parker and Kareiva, 1996; Warwick et al., 1999; Paltridge, 2000; Kjellsson and Strandberg, 2001) make suggestions and offer guidelines and protocols for the development, monitoring and release of genetically engineered plants, with the intention of minimizing these potential risks.

Conclusion

With increasing numbers of studies being conducted, knowledge about the genetics of invasive species, from genetically "ideal" invaders to changes in invasive species over time, is rapidly growing and will continue to provide insights and improve powers of prediction and management of invaders. Although no concrete rules have been developed as a result of the genetic research being conducted on invasive species, general patterns and trends are starting to emerge, and previously unfore-

seen consequences of invasions are now being identified at the molecular as well as the ecological level. Genetic approaches to the study of invasive species are likely to become an increasingly important tool in understanding the processes of invasion, especially with expanding global commerce and movement of plants and animals around the world, and with the growing numbers of genetically engineered crops being developed and utilized. Although Williamson (1996) states that invasions are fast and evolution is slow, the factors that affect evolution of species (particularly gene flow and "mutation" via genetic engineering) are being altered by humans at a rapid pace, and molecular techniques, along with more studies of quantitative ecological genetics, may provide the best method of detecting and understanding the genetic changes and consequences of current and future invasions.

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Association of *Armillaria mellea* with Mamane Decline at Pu'u La'au

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Mamane (*Sophora chrysophylla*) occurs in almost pure stands on the eastern, northern, and western slopes of Mauna Kea (Scott et al., 1984), and is abundant on the southern slopes (Banko et al., in press). Over the course of the 1900s, however, these stands have suffered deprivation from the introduction of alien species such as feral sheep, goats, mouflon sheep, and several species of alien weeds. In addition to habitat competition from the weeds, grasses (the nonnative grasses in particular) increase the wildfire danger to unnatural levels, posing a direct threat to mamane forests (Scowcroft and Conrad, 1992). The endangered palila (*Loxioides bailleu*), once more widely ranging but now known only from the upper slopes of Mauna Kea, depends for its subsistence chiefly on immature mamane seeds (Scott et al., 1984) that it expertly gleans from green seedpods. Thus, threats to the well being of mamane constitute in turn threats to the survival of palila. However, resource managers and scientists involved with the recovery of palila populations are currently concerned with an additional, heretofore relatively little understood, threat.

Avian scientists who frequent the subalpine dry mamane forest at 6,500-9,500 ft. on the western slope of Mauna Kea near Pu'u La'au (see Juvik et al., 1993) have been aware of its progressive deterioration for a number of years. This site is characterized by an almost pure, but open, scattered stand of mamane with tree height less than 26 ft. (8 m). Because of the lack of recognizable disease signs, such as conks on the trunks, only in recent years has the problem come to the attention of plant pathologists.

Rather than old age-related senescence, the decline appears in trees that should otherwise be vigorous and healthy. cursory observation indicates that many, if not most trees at the site show symptoms of decline to some degree, from dead twigs and branches and sparse foliage, death of major trunk branches to death of the en-

tire tree. Recently killed trees remain standing, as evidence of their premature demise. Other than this, no cause for the decline is apparent to the casual observer.

The possible role of drought in contributing to the decline was considered. Soils of the Pu'u La'au site are poorly developed with low amounts of organic matter and little water-holding capacity. Annual rainfall averages 511 mm [20 inches] (Scowcroft and Conrad, 1992; Juvik et al., 1993). However, the wood under the lower trunk bark of declining trees was found to be surprisingly moist, indicating that water deficiency was probably not a factor. A wood-boring cerambycid beetle grub was found in the lower trunks of some of the declining trees. However, our failure to consistently find the larvae in all unhealthy trees sampled suggested that this beetle larva was not the primary cause of the decline.

In cutting away the bark of the lower trunk at ground level, we observed white mycelial fans on the cambium and distinctive dark rhizomorphs on the roots of the fungus *Armillaria mellea*. *Armillaria* is a serious forest pathogen of worldwide distribution and with a broad host range of over 600 species, causing root rot in both coniferous and hardwood trees (Raabe, 1962, 1966). Raabe (1966) reported: "In Hawai'i, the fungus has been found attacking koa (*Acacia koa*) on the islands of Kaua'i and Maui, and at Volcano, Kukaiau, and Honau-nau on the island of Hawai'i. In addition, in the Volcano area, it was found on 'ohi'a (*Metrosideros polymorpha*) and in an area above Volcano, it was found killing young plants of *Pinus montezumae*, *P. echinata*, *P. pinaster*, and *P. halepensis*, where these plants were set out on land previously cleared of koa." The occurrence of *Armillaria* on both native hosts (koa and 'ohi'a) and nonnative pines should be noted. Bega (1979), listed *A. mellea* among a number of "higher" heart and root rotting fungi on several thousand acres of deteriorating koa stands on heavily grazed rangeland in the Keanakolu, Halepiula,

and Spring Water Camp areas at an elevation of 5,000 to 6,000 ft. on the northeast side of Mauna Kea. At this site, *Armillaria* caused a stringy white root and butt rot, producing the characteristic black rhizomorphs (string-like structures comprised of fungal strands) and white mycelial fans by which the fungus could be identified and distinguished from the other fungi present. These other fungi included *Phaeolus schweinitzii* (= *Polyporus schweinitzii*), *Polyporus sulphureus*, *Pleurotus ostreatus*, and *Ganoderma* sp. These fungi readily produce prominent, shelf-like conks (fruiting bodies) on the trunks of infected trees, which are the only means whereby the respective fungi can be identified in the field.

In contrast to the production of conks, at infection sites in most regions other than Hawai'i, *A. mellea* produces clusters of honey-colored fruiting structures (sporophores or mushrooms) from the base of infected trees. In regions where the fruiting structures are common, their color has given *A. mellea* the common name "honey fungus." However, sporophores have not been found in Hawai'i for an unknown reason (Bega, 1979).

Raabe and Trujillo (1963) reported *A. mellea* from a Christmas tree planting at about 6,000 ft. elevation on the slopes of Mauna Loa, Hawai'i Island. The fungus was found infecting, and apparently killing, 2-4 year-old saplings of several species of pine that had been set out following the clearing of the land of koa 2 years previously. In a nearby area at about 4,500 ft., a single root of a large, uprooted koa tree was also infected by *A. mellea*.

Armillaria typically enters its host from the soil through the roots and moves between the bark and the xylem tissue (i.e., the hardwood). The fungus encompasses the root and girdles it, and may also move into and girdle the lower part of the main stem, effectively killing the tree. In Hawai'i, as mentioned above, *Armillaria* root rot produces no definite external symptoms whereby these diseases can be diagnosed. In fact, the lack of such symptoms and signs serves to distinguish it from diseases caused by other wood rotting fungi that produce conks, as noted above. Plants infected with *A. mellea* may appear unhealthy, have yellow leaves, sparse foliage, and have dead branches. Once infected, trees may live for an extended period while slowly declining, or they may be killed rapidly (Raabe, 1966). Although *Armillaria* root rot has been reported from some tropical countries, the disease is more common in temperate climates. Where it occurs in the tropics, it is usually found at upper elevations where cooler conditions prevail. In Hawai'i, the disease has been reported on the islands of Kauai and Maui, and is known from several different locations on the island of Hawai'i, all at elevations of

3,000 ft. or above (Raabe, 1962, 1966; Raabe and Trujillo, 1963).

In a 1974 compilation of the known hosts of *A. mellea* in the islands, Laemmlen and Bega (1974) listed 23 species, including mamane, among 11 other woody native Hawaiian species. Thus, whereas we have not directly demonstrated the pathogenicity of the fungus recovered from diseased mamane trees at the Pu'u La'au site, consideration of the above observations leaves little doubt that *Armillaria* root rot is the cause of the dieback.

At present there is no known effective control of *Armillaria* root rot, particularly where it occurs in natural stands of native forest, such as the Pu'u La'au forest. Control measures among commercial timber stands or tree crops usually emphasize the use of resistant plants.

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Hybridization and the Potential Consequences for Rare Plant Species

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The phrase "conservation of biodiversity" is being heard around the world. Rates of extinction have climbed to a new high – instigating a rally of efforts based around conservation of rare species. The increased rate of species extinctions is mainly due to anthropogenic actions including habitat fragmentation and destruction (Wilson, 1988). Introduction of exotic species is another anthropogenic action threatening native species and habitats around the globe. Environmental change, loss of habitat, competition with invasive species, demographic stochasticity as well as inbreeding depression and low genetic diversity are often analyzed and viewed as key reasons for extinction of rare species. Little research, however, has examined the threat to rare, native plant species resulting from hybridization with introduced taxa.

If conservation is the goal, then it is important to accurately determine the key threats to rare and native species existence. Hybridization may be one of these key factors, especially given the magnitude of habitat modification and non-native species introductions in recent years. These actions often bring previously isolated plant taxa into direct contact, which greatly increases the likelihood of hybridization. Hybridization may promote extinction of a rare plant species by reducing the ability of individuals in these populations to replace themselves thereby inhibiting the growth of the population (Levin et al., 1996). With continued hybridization and introgression, the rare species may even be genetically assimilated by the more abundant congener and, thus, "lost" as a distinct and unique species (Allendorf et al., 2001).

Hybridization

Hybridization has been defined as "interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations" (Rhymer and Simberloff, 1996). Most commonly, hybridization refers to mating among differ-

ent species. Evolutionarily, hybridization can result in rapid change by producing novel gene combinations that may lead to increased genetic variation, increased fitness, and adaptation to new environments in existing taxa (Rhymer and Simberloff, 1996). Natural hybridization has most likely played an important role in plant evolution and speciation (Ellstrand et al., 1999).

Historically, interspecific hybridization in the wild was believed to be a rare or novel phenomenon (Anderson, 1948). Although, geographic isolation of related taxa was believed to limit the occurrence and impacts of hybridization, it was also commonly believed that interspecific hybrids were sterile (Zirkle, 1935 as stated in Anderson, 1948). Thus, even if hybridization did occur, the hybrids would not persist. It is currently understood that hybridization among related species can often result in fertile or semi-fertile individuals and that hybridization in the wild has played a role in speciation events.

Anthropogenic Affects

Anthropogenic actions may be greatly increasing the rate of interspecific hybridization. Currently, introduced plant taxa are commonly brought into contact with rare and native species through human action such as introduction of nurse stocks and garden cultivars, creation of disturbed habitat corridors via road building, cultivation of land for agricultural purposes, and accidental introduction (Levin, 1996; Freas and Murphy, 1988). In fact, there are many examples of introduced weeds hybridizing with native species. In Hawaii, the introduced *Rubus rosifolius* hybridizes with the endemic *R. hawaiiensis* (Randell 2000) and *Gossypium barbadense* hybridized with the endemic *G. tomentosum*. In Florida, the tetraploid *Lantana camara*, an escaped ornamental, has hybridized extensively with the endemic diploid *L. depressa*. The triploid hybrids are quite vigorous and yet manage to retain the local adaptations of the native species (Sanders, 1987 as quoted in Levin et al., 1996). Further, many endangered sunflower (*Helianthus*) spe-

cies are threatened by hybridization with the weedy *H. annuus* that has spread widely due to human sowing and disturbance (Rogers et al., 1982 as cited in Rhymer and Simberloff, 1996).

Hybridization rates may be heightened when species that are brought together by human action have not evolved reproductive barriers against hybridization. Reproductive barriers may evolve in sympatric populations of closely related species during the natural process of speciation (Raven, 1980). These barriers are one factor that helps maintain species identities. However, reproductive barriers would not necessarily be selected for, or evolve in, allopatric and insular populations.

Species on islands appear to be particularly vulnerable to hybridization due to their small numbers and the ease with which they interbreed (Levin et al., 1996). Island species tend to be reproductively isolated by habitat rather than by genetic or chromosomal barriers (Rhymer and Simberloff, 1996). In other words, insular species tend to be less genetically divergent and have weaker crossing barriers that make them more prone to interbreeding (Crawford et al., 1987 as cited in Levin et al., 1996). In fact surveys by Rieseberg and Gerber (1995) of the hybrid flora of Hawaii revealed the occurrence of hybridization in close to 40 genera and 23 plant families. The majority of these hybrid combinations involved endemic, and often rare species of *Cyrtandra* (67 hybrid combinations), *Dubautia* (24) *Bidens* (10 and *Clermontia* (8) (Rieseberg and Gerber, 1995). Increasing human disturbance and introduction of related species to islands amplifies the risk of interspecific hybridization between native and introduced species.

Introgression

Often hybridization is coupled with introgression. The term introgressive hybridization was coined in the 1940's by Edgar Anderson to describe the phenomenon in which hybrid offspring tend to "backcross" or breed with one or both of the parental species (Anderson, 1948). Introgression results in gene flow and mixing of gene pools between previously separated species. Mixing of gene pools, particularly in reference to hybridization between introduced and native taxa, has been given many names including: "contamination," "infection," "genetic deterioration," "genetic swamping" and "genetic pollution" (Rhymer and Simberloff, 1996). Introgression often occurs unequally and it has been demonstrated that hybrids tend to backcross preferentially with the more abundant parental species (Potts, 1986; Rieseberg et al., 1996; Caraway et al., 2001).

A well-known case of hybridization with introgression

in Hawai'i between an introduced and native species is the case of the mallard duck (*Anas platyrhynchos*). The mallard duck has been introduced to many areas around the world including Hawaii. In Hawai'i, there has been extensive hybridization and introgression among introduced mallards and the endangered, endemic koloa (or Hawaiian duck; *A. wyvilliana*). In fact, due to continued hybridization and introgression, it is feared that no "pure" koloa remain on the island of O'ahu (Michael Silbernagle, personal communication).

Generations of hybridization and backcrossing can erode the genetic integrity of a rare species (Levin et al., 1996). In fact, continued introgression may result in "genetic assimilation" or the incorporation of genes of one species into the gene pool of another species (Rhymer and Simberloff, 1996; Allendorf et al., 2001). Genetic assimilation may dilute allelic frequencies of a rare plant species eventually leading to deterioration of the genetic integrity of this species. This may cause the loss of genotypes of ecologically specialized plant populations. Small, isolated populations that hybridize with a more abundant species and that produce vigorous, fertile hybrids are most at risk of being genetically assimilated. Studies of *Cerocarpus trasskaie* (Rieseberg and Gerber, 1995), *Argyranthemum coronopifolium* (Bramwell, 1990), and *Atriplex tularensis* (Freas and Murphy, 1988) are examples from plant systems that illustrate that extinction of a rare species (via genetic assimilation) by an introduced species is a real, not just theoretical, threat.

Hybrid Fitness

As previously stated, it was originally believed that F_1 hybrid individuals are always sterile (Zirkle, 1935). This would prevent the introduction or introgression of novel genes into gene pools of either parental population. However, it is now acknowledged that hybrids demonstrate a range of fertility from complete sterility to complete interfertility (Anderson, 1948; Rieseberg, 1996). F_1 and later generation hybrids have been noted to demonstrate either hybrid vigor (Graham et al., 1995; Milborrow, 1998) or reduced fitness (Raven, 1980) as compared to the parent species.

Hybrid vigor, or heterosis, can be defined as the increase in growth, size, fecundity, function, yield, or other characters in hybrids over those of the parents (Allaby, 1998). Several studies have indicated that spontaneous hybridization between crops and related wild species occurs readily and results in hybrid plants, that exhibit hybrid vigor (Arriola and Ellstrand, 1996; O'Brien et al., 1967). Hybrids expressing high fitness parameters are not relegated to agricultural setting. Evidence of hybrid

fitness in natural populations has been demonstrated in *Anigozanthos* (Hopper, 1978), *Iris* (Hodges et al., 1996), and *Artemisia* (Graham et al., 1995) among others.

Millborrow (1998) has proposed a biochemical mechanism for the increased size and growth rates of heterozygote hybrids as compared to two homozygous parental taxa. The mechanism suggested for this "hybrid vigor" includes a "relaxation" of genetic controls that regulate growth due to heterozygosity. This hypothesis assumes that the functioning of several randomly segregating factors restricts growth. Recombination of different alleles of homozygous parents could potentially result in a combination that "relaxes" the tight growth control mechanisms. This hypothesis was further proposed to account for homeostasis of hybrids in response to environmental changes.

Experimental studies of competitive interference (O'Brien, 1967; Hopper, 1978) demonstrate that hybrids may not only be vigorous in their growth, they may also be effective competitors. In these cases, hybrid individuals exhibited greater survivorship and biomass as compared to one of the parental species. Further, one of the parental species had decreased survivorship and biomass when grown with the hybrids. If a hybrid cross is the result of a native/alien hybridization, and if either the introduced taxa or the resultant hybrid plants exhibit stronger competitive ability than the native taxa, the result could be the rapid displacement of the native species.

On the other hand, hybridization and introgression can also result in reduced hybrid fitness and outbreeding depression (Rieseberg, 1991; Allendorf et al., 2001). Outbreeding depression is the reduction in fitness of first generation as well as later generation hybrids and backcrossed offspring. Outbreeding depression is usually caused by meiotic abnormalities or disruption of co-adapted gene complexes (Dobzhansky, 1948 as quoted in Rieseberg, 1991). For example, segregation difficulties during meiosis may occur due to differences in diploid number of chromosomes in the parental species (Rhymer and Simberloff, 1996). If the F_1 or later generation hybrids are partly sterile or have reduced vigor, then the rare parental species may be endangered by outbreeding depression.

Ellstrand (1999) points out that outbreeding depression from detrimental gene flow will reduce the fitness of a locally rare species that is mating with a more abundant congener. The rare species may have reduced fitness due to "spending" vital resources such as pollen and ovules on the production of unfit hybrid individuals at the expense of production of "pure" progeny. As only a small percentage of the pollen produced is required to

fertilize ovules, the primary cost of outbreeding depression in plants appears to be reduced seed set by the maternal parent (Reieseberg and Gerber, 1995).

Hybrid Zones

It is often observed that hybrids tend to occupy, or are restricted to, disturbed areas or areas at the boundary between the two parental habitats (Graham et al., 1995). The term "hybrid zone" is often used to describe this region in which genetically distinct populations meet, mate, and produce hybrids (Barton and Hewitt, 1989). Formation of hybrid zones may result from secondary contact between populations that have differentiated in allopatry (Hodges et al., 1996). Hybrid zones between divergent taxa sometimes remain distinct despite gene exchange at narrow zones of contact (Freeman et al., 1991).

Explanation for maintenance of hybrid zones includes the "bounded hybrid superiority" hypothesis. This hypothesis proposes that hybrid zones are areas of ecological transition where hybrids exhibit superior fitness to either parental type (Arnold, 1992). In other words, due to increased genetic variability via recombination, hybrids are able to occupy niches unfavorable to either parent (Anderson, 1948; Hopper, 1978). Thus, within this zone there is no selection against hybrids and consequently reproductive isolation does not evolve allowing the zone to persist (Freeman et al., 1991).

A second theory for the creation and maintenance of hybrid zones is the "dynamic equilibrium hypothesis" (Barton, 1979). The dynamic equilibrium theory is based on the concept of outbreeding depression. This theory assumes that hybrids have lower fitness than either parent regardless of habitat, and thus are selected against in the parental habitat. This selection against hybrids restricts them to the zone between the parental habitats. A third model is that of the "tension zone" and is based on the assumption that natural selection acts against hybrids and restricts them to zone of tension between the parental populations (Burke et al., 1998).

Limited gene flow by means of pollen and seed dispersal has also been cited as causes for creation of hybrid zones. A study of two species of *Anigozanthos* and their F_1 hybrids determined that pollen and seed flow limitations were the main underlying reason why hybrids are found in confined distributions (Hopper, 1978).

However, habitats are often not stable and/or two species are brought together by human action or disturbance. Instead of having an intermediate habitat that supports a hybrid zone there may now be a mosaic of fragmented microhabitats and/or the introduction of a superior competitor. Spatial and ecological separation of

two previously isolated species may be completely broken down and may result in production of a hybrid swarm. The term "hybrid swarm" has been used to describe areas in which extensive hybridization and introgression among hybrids and between the hybrids and both parental species is occurring. Hybrid plants in these areas may appear intermediate between parental types or exhibit any combination of parental characters. Hybridization and introgression in these swarms may result in fusion of two populations into a single population that is highly variable and in which "pure" individuals of either species are infrequent or absent. If both species are in small, localized populations and contribute similarly to a hybrid swarm, the genetic integrity of both species may be lost (Levin et al., 1996). However, if one species is dominant in an area where a hybrid swarm is forming, the minor species often declines over time. This process is a threat to the conservation of rare species and their unique phenotypes and genotypes.

The Demographics of Hybridization

Introduction of and subsequent hybridization with non-native species can have dramatic effects not only on the genetic structure of the native species, but also on the population demographics of a native species. Hybridization makes a population vulnerable due to gametic wastage, reduced seed set, production of ill-fit progeny and pollen swamping (Levin et al., 1996). In small fragmented populations, lack of plentiful conspecific individuals may increase the chance of interspecific hybridization, especially if the introduced taxon is more abundant (Byers and Meagher, 1992). Both lack of available mates and available habitat have been described as limiting the population growth and continued survival of rare species (Lande, 1988; Eriksson and Ehrlen, 1992).

Production of hybrid seed and pollen "swamping" of a rare species by an abundant introduced species may result in decreased rates of "pure" progeny. This process has been examined in a study by Potts (1986) of *Eucalyptus risdonii* and *E. amygdalina*. Regeneration of the two species of *Eucalyptus* and their hybrids was charted after a wildfire. Results showed that a large proportion of F₁ hybrids were produced from seed of the less abundant species *E. amygdalina*. It was inferred that this was due to fertilization of *E. amygdalina* individuals by the plentiful pollen of *E. risdonii*. Thus, the more abundant species was reducing the rate of "pure" progeny of *E. amygdalina* via "pollen swamping." Rare species cannot afford such "gametic wast-

age" (Levin et al., 1996) as survival and integrity of the species may depend on high rates of reproduction.

Theoretically, a situation involving a rare native species and an aggressive and abundant introduced congener could result in the introduced species swamping out the native species via increased pollen flow, higher reproductive fitness, and unequal rates of hybrid seed being produced by each taxon. If these forces are not compensated for by regeneration via immigration of seeds or pollen of the native species, it could have a detrimental effect on survival of the native species. Human impact continues to destroy and fragment vital habitat causing populations of rare species to become excessively small and fragmented. Geographic isolation of populations (via habitat fragmentation) hinders regeneration of population size due to a decrease in migration among populations via seed or pollen dispersal (Lande, 1988). As populations of rare species tend to be geographically isolated the effects of increased gene flow and competition from abundant introduced taxa are not likely to be counterbalanced by immigration of the native species.

Conclusion

In the absence of hybridization, the interaction between a native and introduced species is essentially a competitive one. Hybridization resulting in vigorous hybrids creates a two-fold threat to a rare species. Reproduction via hybridization results in loss of "pure" progeny or "gametic wastage." Concurrently, vigorous hybrids may be able to effectively compete or even out-compete individuals of the native taxon.

A study by Huxel (1999) suggested that "in cases where related taxa are able to interbreed, introductions may lead to the introduced taxa dying out, coexistence, new hybrid taxa or extinction of the native taxa." If the introduced species happens to be a stronger competitor, it can potentially "outcompete" and displace the native taxon. Adding hybridization and introgression to the equation increases the chances of displacement of rare species due to genetic "swamping" and added competition from hybrids. A native species could theoretically be overwhelmed and displaced in a short time period if immigration of the introduced species and the rate of hybridization and introgression are all high and there is low replacement or immigration between populations of the native species (Huxel, 1999). Although few studies have documented the displacement of native species via hybridization, studies by Rieseberg and Gerber (1995), Bramwell (1990), and Freas and Murphy (1988) show that it is quite possible. Effective

conservation strategies not only need to identify the life history stages that appear to restrict a rare species persistence and growth, but must also identify all outside threats. These threats include not only habitat destruction and loss, but also the threat of hybridization and introgression with introduced species.

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MINUTES OF THE HAWAIIAN BOTANICAL SOCIETY

October 1, 2001

Guests: Rene Johanssen, Molokai resident, Cheryl Seaman

Minutes: Approved as read.

Treasurer's Report: Treasurer's report given for the months of June to August

June, start: \$2182.93

Income: dues: \$197 (and change)

Posters: \$21

B.Krauss: \$72.08

Life Member Fund: \$22.40

Interest: \$29.50

Outgo: postage: \$82.00

Copies: \$44.58

Refreshments: \$34.46

Stationary: \$29.11

September, end: \$2853.68 (I know it probably doesn't balance out, as I think I missed a few numbers).

Announcements:

- Alvin Yoshinaga gave away *Delissea rhyti-*

dosperma seedlings from Keith Robinson's preserve on Kaua'i.

- Betsy Gagne announced an alien plant control service trip to Manuka NAR on the Big Island over Veteran's Day weekend (Nov 10-12); contact Betsy for more details.
- T-shirts, mugs and tote bags from the 2001 SCB/Hawaii Conservation Conference are STILL available from the PCSU office in St. John 409 or from Chuck Chimera (chimera@hawaii.edu).

Old Business:

- Nominating committee is still looking for new board members.

New Business:

- None

Plant of the Month and Speaker:

- Web Site of the Month: Hawaiian Native Plant Propagation (www.ctahr.hawaii.edu:591/hawnprop/, Eileen Herring).

Topic and Speaker:

- Palms- The Tree of Life, Melany Chapin, National Tropical Botanical Garden.

November 5, 2001

Guests: Sheila Foreman, Kanoa Kimble

Minutes: Approved as read.

Treasurer's Report:

Start: \$2853.68

Expenses: \$323 (mostly newsletter expenses)

Income: \$80.31

End: \$2610.99

Announcements:

- Carol Annable announced that Waimea Arboretum is having a Christmas plant sale on December 8th.
- Betsy Gagne announced that there were still a few openings for an alien plant control service trip to Manuka NAR on the Big Island over Veteran's Day weekend (Nov 10-12); contact Betsy for more details.
- Ray Baker announced that the Volunteer Stewardship Network would be rescheduling its service trip leader training for the beginning of 2002; more to follow.
- Ray Baker also announced that Lyon Arboretum would be having a plant sale on November 17th from 9:00 a.m.-2:00 p.m.
- T-shirts, mugs and tote bags from the 2001 SCB/Hawaii Conservation Conference are STILL YET available from the PCSU office in St. John 409 or from Chuck Chimera (chimera@hawaii.edu).

Old Business:

- Vickie Caraway announced the nominees for the 2002 Hawaiian Botanical Society board as follows:

President: Susan Harbin

Vice President: Joan Canfield

Secretary: Chuck Chimera

Treasurer: Ron Fenstemacher

Board: Jeff Preble and Brandon Stone

Nominations are still being accepted. Please contact Vickie Caraway if you or anyone you know may be interested.

New Business:

- Vickie Caraway reported that the Board of Land and Natural Resources would be holding a public meeting on Friday, November 16th in Kona to discuss the future of the lease of Pu'u wa'awa, one of

the last and nicest patches of dryland forest left in the state. Possibilities include a return to ranching, greater access to hunting, or protection and conservation. Vickie motioned that Bot Soc send a representative (Betsy Gagne on vacation) to testify on behalf of the conservation of the area. The motion was seconded and passed unanimously. Good luck!

Plant of the Month: Nuts about Nutmeg and Mad about Mace: The Ethnobotany of *Myristica fragrans* by Jodi Stevens, UH Botany Department.

Topic/Speaker: Mexican Mariachi, Big Bromeliads & Panamanian Peccaries: Links Between Culture & Conservation in a Neotropical Rainforest by Dr. Tamara Ticktin, UH Botany Department.

December 3, 2001

Guests: Jean Larr

Minutes: Approved as read.

Treasurer's Report:

Start: \$2610.99

Expenses: \$160.29

Income: \$53.86

End: \$2504.56

Announcements:

- Betsy Gagne announced that she had free watershed posters for distribution.
- Carol Annable announced a plant sale at Waimea Arboretum on December 8th.
- Betsy Gagne announced that there has been no decision made on the status of Pu'uwa'awa'a, but that 59 people signed up to testify on behalf of conservation.
- Betsy Gagne also announced that the Honolulu Academy of Arts was displaying "Remains of A Rainbow" throughout the month of December.
- Chuck Chimera announced the publication of a new newsletter.
- T-shirts, mugs and tote bags from the 2001 SCB/Hawaii Conservation Conference are STILL YET available from the PCSU office in St. John 409 or from Chuck Chimera (chimera@hawaii.edu).

Old Business:

- Carol Annable informed the society that we had 64 renewals as a result of the membership drive, and got several new members as well.

New Business:

- The "election" results for the 2002 Hawaiian Botanical Society executive committee are as follows:

President: Susan Harbin (hail to the chief!)

Vice President: Joan Canfield (welcome aboard Joan)

Secretary: Chuck Chimera (t-shirts anyone?)

Treasurer: Ron Fenstemacher (mahalo for taking the job nobody wants)

Board: Jeff Preble and Brandon Stone (ready to step in and fill any of the above positions, especially secretary, at a moment's notice).

- Mahalo nui loa to Dr. Don Gardner, outgoing Vice President, for the outstanding job he did throughout 2001 with both the selection of speakers AND the publication of the newsletter. Don will be sorely missed.

Plant of the Month: Kahili Ginger: Battling the fragrant invader, Rob Anderson, USGS-Biological Resources Division.

Topic/Speaker: Pu'u Kukui Watershed: The Bleeding Edge of Resource Management, Randy Bartlett, Maui Land and Pineapple.

**TREASURER'S REPORT
JANUARY TO DECEMBER 2000**

The Hawaiian Botanical Society had an unusual financial year. Annual dues income was way off, but as no Newsletters were issued, it's a draw. The Life Member Fund finished about \$5.00 short of its ultimate financial goal, so by early next year it starts leaving black ink on the Annual Fund's bottom line. Awhile ago, longtime member Bea Krauss kindly remembered the Society in her will. Her legacy was realized this year and went to the Neal-Miller-Krauss Fund.

The treasurer would like to thank Jonel L. Smith for her thorough financial audit of the Society's books for 1999.

Finally, it is with great sorrow to note the sudden passing of two distinguished and longtime life members, William Hoe and Charles Lamoureux. While the Society can say or do little to beguile friends and loved ones from such overwhelming loss, all our hearts hold profound sympathy for each and every one weathering difficult times.

2000 Annual Fund Summary:

<u>Income</u>		<u>Outgo</u>	
Annual Dues	\$315.00	‡ Annual Payment	\$250.00
Donation	\$200.00	Science Fair	\$248.32
Plantasia	\$60.00	Postage	\$235.00
75 th Anniversary	\$39.55	Memoriam	\$100.00
Interest	<u>\$38.93</u>	Copying	\$95.27
Total	\$653.48	Stationery	\$22.49
		Refreshments	<u>\$20.01</u>
		Total	\$971.09

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$$\begin{aligned} \text{Beginning Balance} + \text{Income} - \text{Outgo} &= \text{Ending Balance} \\ \$3118.00 + \$653.48 - \$971.09 &= \$2800.39 \end{aligned}$$

The net loss for the Annual Fund in 2000 is \$317.61.

2000 Annual Dues Summary:

Student,	3 x 1 yr	\$15.00
Individual,	16 x 1 yr	\$160.00
	2 x 2 yr	\$40.00
Family,	5 x 1 yr	\$60.00
Institutional	1 x 1 yr	\$20.00
Cash		<u>\$20.00</u>
Total		\$315.00

Life Member Fund Summary:

	<u>Income</u>	<u>Outgo</u>
Interest	\$367.20	none
'99 Life Dues (2)	\$360.00	
'00 Life Dues (2)	\$360.00	
‡ Annual Payment	\$250.00	
Donation	<u>\$150.00</u>	
Total	\$1487.20	

$$\begin{aligned} \text{Beginning Balance} + \text{Income} - \text{Outgo} &= \text{Ending Balance} \\ \$5768.68 + \$1487.20 - \$0.00 &= \$7255.88 \end{aligned}$$

The LMF began 2000 with a target sum of \$7020.00. The Society gained three life members during the year (3 x \$180.00 = \$540.00) but lost two (2 x \$150.00 = \$300.00), resetting

the yearend LMF target sum to \$7260.00. The difference between this target sum and the yearend balance is \$4.12.

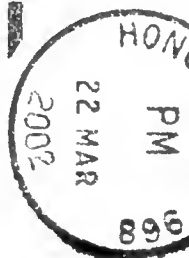
One life membership was realized too late to augment the LMF within the year and will join the account at its next maturity date in January 2001. These pending dues along with whatever interest the account realizes exceed \$4.12. In other words, the LMF achieves its financial goal and is fully funded in January 2001, finally to generate income for the Annual Fund

Respectfully Submitted,

R. Fenstermacher

R. Fenstermacher, Treasurer

NEWSLETTER OF THE HAWAIIAN BOTANICAL SOCIETY
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