Landscape modification and impact on specific and genetic diversity in oceanic islands

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Species diversity in oceanic island archipelagoes is caused by many factors. The equilibrium theory of island biogeography emphasizes size of islands and distance from source areas as important factors. However, other factors also influence species diversity in islands. Speciation within the archipelago, unequal ecological partitioning, different rates of evolution, and variation in inter-island dispersal capabilities, are some additional factors not considered under the initial model. Another factor is the impact of history, which can be viewed from many dimensions, including phylogenetic history (history of speciation), but the type most often discussed in oceanic archipelagoes is human impact. Humans have disturbed natural island ecosystems through direct harvesting of plants and animals, introduction of invasive exotic species, and deliberate and accidental use of fire. Historical aspects of natural landscape modification are also significant. Oceanic islands of volcanic origin arise from the sea floor and emerge above the sea, undergoing a rapid modification through colonization by numerous life forms. These islands gradually subside due to cooling and contraction of the oceanic crust, and they are eroded by wave action, wind, and rain, finally disappearing under the ocean after approximately six million years. An oceanic island that is four to five million years old may have lost 75-95% of its surface area. This areal loss also results in loss of habitats, reduction in the breadth of ecological zones, and loss of species diversity. It must also lead to reduction in population size in many species. It is challenging, therefore, to interpret patterns of genetic variation within and among populations on older islands. Low levels of genetic variation in island populations are often interpreted as resulting from a founder event during initial dispersal and establishment. It is difficult to distinguish this influence from genetic drift caused by reduction in population size due to diminishing landscape and loss of ecological zones.

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Introduction

Oceanic islands have long been considered as natural laboratories for the study of plant evolution. Because of their physical setting, land masses surrounded by large expanses of ocean, they invite hypotheses regarding how and from where endemic flora has arrived and how it has diversified after colonization. Islands have stimulated numerous generations of biologists

going back to Darwin (1842) and Wallace (1871), and many theories of island biogeography and speciation have emerged. In recent years, quantitative approaches to phylogeny reconstruction, more rigorous biogeographic analyses, and molecular markers have provided many new insights.

Many theories have been advanced to explain levels of species diversity in oceanic islands. Because of their simplicity, island archipelagoes have attracted attempts to model and explain numbers of species, both native, endemic, and even invasive. An important attempt to explain species diversity was provided by MacArthur and Wilson (1967). Emphasizing simple and manageable dimensions of island size and distance from source areas, they provided an equilibrium model for levels of species number based on accompanying rates of extinction and colonization. It is well known (*e.g.*, Case & Cody 1987; Williamson 1989) that this model, however stimulating as an example toward quantitative attempts to model species diversity, fails to predict accurately the levels of actual species number in island archipelagoes because of lack of additional information, including levels of inter- and intra-island speciation, ecological partitioning of the island environment, different dispersal abilities, and so on.

In addition to these biological factors that influence species diversity in islands, historical factors are also very important. The obvious influences are those due to human disturbance during historical time, often documented when speaking about island diversity. Easter Island provides a classic case of ecological alteration due to exploitation already by the Polynesians and subsequent ecological and cultural collapse of the entire plant and human populations on the island (Zizka 1991). Alterations include direct cutting of forests, clearing of land for cultivated crops, burning, introduction of domestic animals (some becoming feral, such as goats and pigs), and introduced plants (some becoming invasive plagues of great menace to the endemic island flora).

Another important factor in reduction of species diversity in oceanic islands is landscape modification due to natural subsidence and erosion. Oceanic islands quickly subside and are eroded by a combination of wind, rain, and wave action. As a result of these impacts, most oceanic islands are short-lived (Nunn 1994). An island four or five million years old has lost a great deal of its elevation, its surface area, its breadth of ecological zones, and its specific and genetic diversity.

The impact that loss of area and habitat diversity may have had upon genetic variation within and among populations of island archipelagoes is poorly understood. It is often assumed that detection of low levels of genetic variation in natural island populations is a consequence of founder effects (*e.g.*, Witter & Carr 1988). While this may be so, it would be difficult to separate this influence from that due to loss of habitat leading to reduction in population number and/or size, and concomitant loss of genetic variation that has accumulated since colonization and proliferation into larger populations. This loss of diversity may simply be a consequence of genetic drift. Focusing on this problem, therefore, is important for understanding processes of evolution (especially speciation, adaptive radiation, etc.) in oceanic archipelagoes.

The Juan Fernandez (Robinson Crusoe) archipelago in the Pacific Ocean is a good, simple system to address these historical factors (Fig. 1). There are excellent historical records (*e.g.*, Woodward 1969; Wester 1991), no previous aboriginal people (Anderson *et al.* 2002), and two principal islands of different ages (c. four million years for Masatierra (Robinson Crusoe), and one-two million for Masafuera (Alejandro Selkirk), based on radiometric dat-

ing; Stuessy *et al.* 1984). The islands harbor more than 400 vascular plant species (more than half of which are introduced; Matthei *et al.* 1993; Swenson *et al.* 1997), including 132 endemics (Marticorena *et al.* 1998). Further, there is considerable information about genetic variation in plant populations (see review by Crawford *et al.* 2001) and the human impact on natural vegetation of the archipelago (Johow 1896; Skottsberg 1953; Greimler *et al.* 2002a, b; Dirnböck *et al.* 2003).

The purposes of this paper, therefore, are to: (1) sketch hypotheses on the subsidence and erosion of the Juan Fernandez archipelago and corresponding loss of land area during the past four million years; (2) demonstrate the historical impacts from humans during the past 400 years; (3) summarize the more recent impacts on the native flora due to invasive species; (4) discuss these factors in context of genetic variation seen in different endemic species in the archipelago and for understanding modes of speciation.

Subsidence and erosion of the Juan Fernandez archipelago

In general, oceanic islands develop and vanish as a consequence of plate tectonics. They either form along divergent plate boundaries (mid-oceanic ridges) or along convergent plate boundaries (near the trench) more or less parallel to the ridge or trench axis (for details, see Nunn 1994). Their lifetime in general does not exceed six million years, that is, very short in comparison to continental areas. There are, however, older islands (*e.g.*, in the Hawaian archipelago; Macdonald *et al.* 1983), and there is some continuum in that new islands emerge as old ones disappear from the same hot spot. Subsidence begins soon after formation, due to plate movement and cooling, thickening and increasing density of the oceanic crust, so that the sea floor subsides iso-

statically (thermo-isostasy) and oceanic islands become gradually submerged. In tropical waters the subsidence is increased by the load of coral reefs which grow upward and thicken as they maintain their shallow water position. Average subsidence rates have been calculated, *e.g.*, for the Marshall Islands (0.20 mm/yr, or 100 m/500,000 yrs; Pirazzoli 1998). Minor changes in sea level are due to polar drift, which causes deformations of the geoid and topography of the sea floor (Pirazzoli 1998) and subsequently a rise of sea level in the northern and a fall in the southern hemisphere (Equator region unperturbed).

Climatic changes also affect the size and shape of the changing oceanic island landscape. These influence the temperature and moisture regime and have induced huge changes in sea levels due to glaciation and deglaciation events. As the global water balance is constant, development or melting of continental ice sheets has been of great importance for sea level changes during the past 20,000 years and certainly for the sequence of glaciations and deglaciations previously. During the past glacial maximum 18,000 years ago, sea level was about 100 m lower than today (Athens 1997). The climatic effects on islands depend on their size and shape and can be very dramatic for small, flat islands, as the proportions (%) of size changes are in reverse proportion to absolute size changes (in km^2). The global Pleistocene cooling correlates with increased aridity in many areas, causing dramatic effects on islands. In Hawaii, *e.g.*, the inversion layer (above which rain clouds do not form) was depressed during the Pleistocene (Athens 1997). Precipitation, therefore, in higher elevations was probably lower than today. There is evidence for downward shifting of vegetation zones in Hawaii during glaciation (at the same time the sea level was 100 m lower; Athens 1997). Coming closer to the present, a dry mid-Holocene period is documented
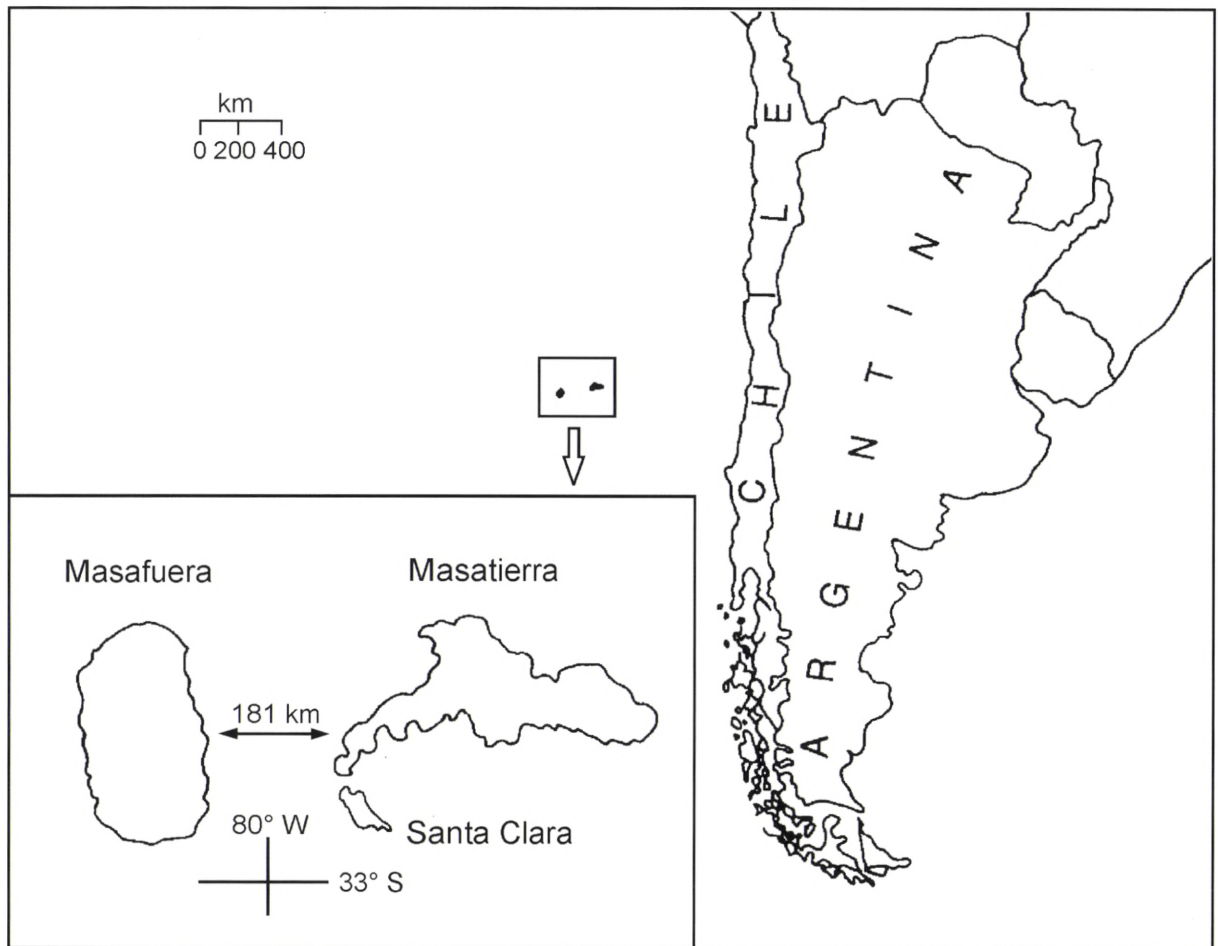
Fig. 1. Map of the Juan Fernandez archipelago.

throughout the Pacific and South America (Athens 1997). This climatic episode could be due to a long-duration ENSO (El Nino-Southern Oscillation).

These geological and climatic effects have had a combined impact on the landscape of the Juan Fernandez Islands (Figs. 2, 3; see also Haberle 2003). The existence of a huge 200 m submarine erosional platform around Masatierra suggests an original island much larger than at present, perhaps reaching to 3000 m and extending nearly 1000 km². As the present height and area of this island are only 980 m and 50 km² (Stuessy 1995), respectively, this represents a tremendous loss of surface area (only 5% remaining; Stuessy *et al.* 1998a). Even more importantly, the loss can be surmised also to have affected ecological zones, with concomitant reductions in number and sizes of plant populations. Masafuera, the younger island (1-2 million years old) shows (Fig. 3) a small 200 m submarine erosional platform very near to the present coast, suggesting that this younger island has not yet entered a major subsidence or erosional phase (it is still a relatively much younger island).
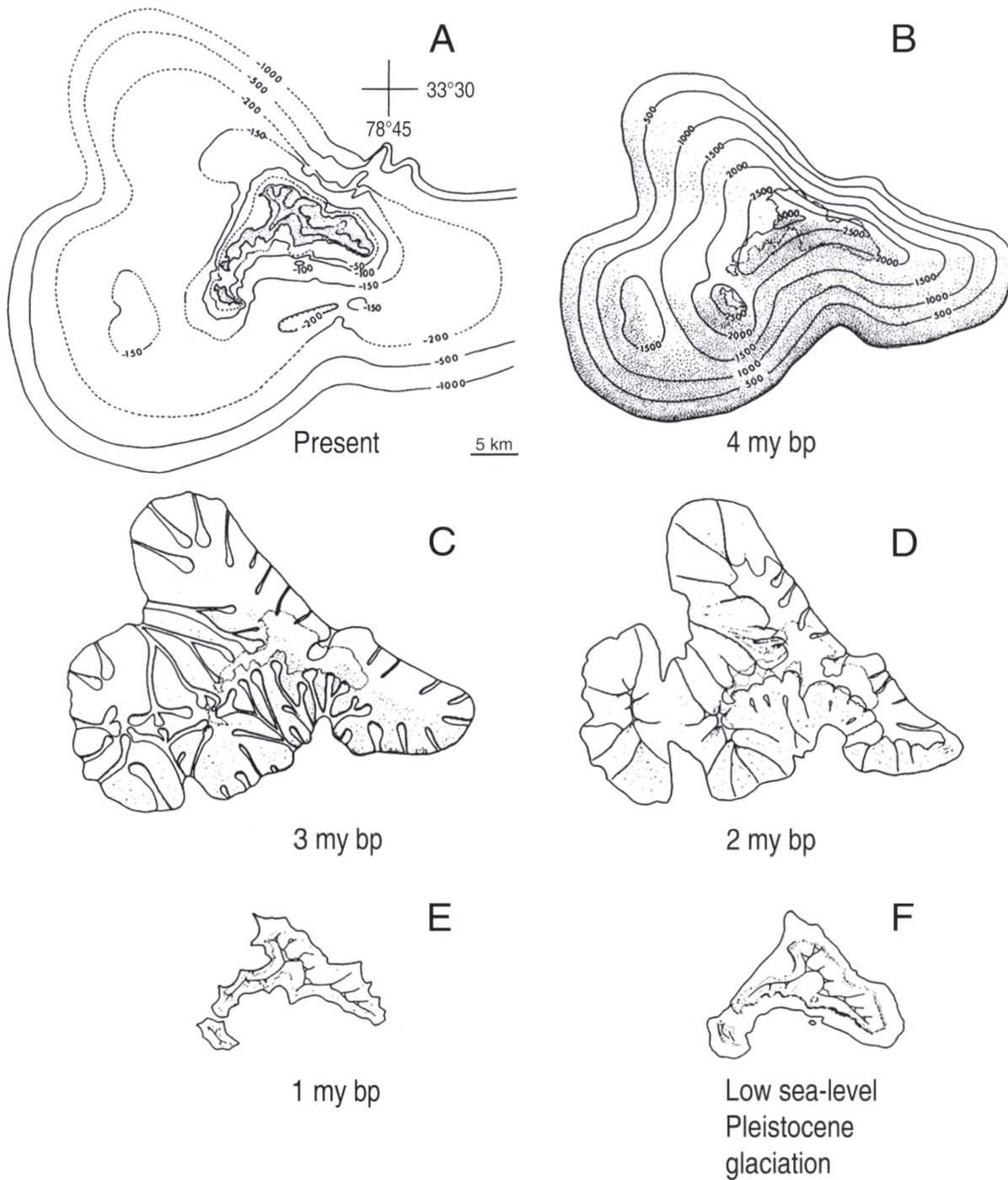
Fig. 2. Hypothesized subsidence and erosion on Masatierra during the past four million years. A, present configuration of island; B, shape of original island, four million years before present (my bp); C, three my bp; D, two my bp; E, one my bp; F, lowering of sea level during Pleistocene glaciation. From Sanders *et al.* (1987).
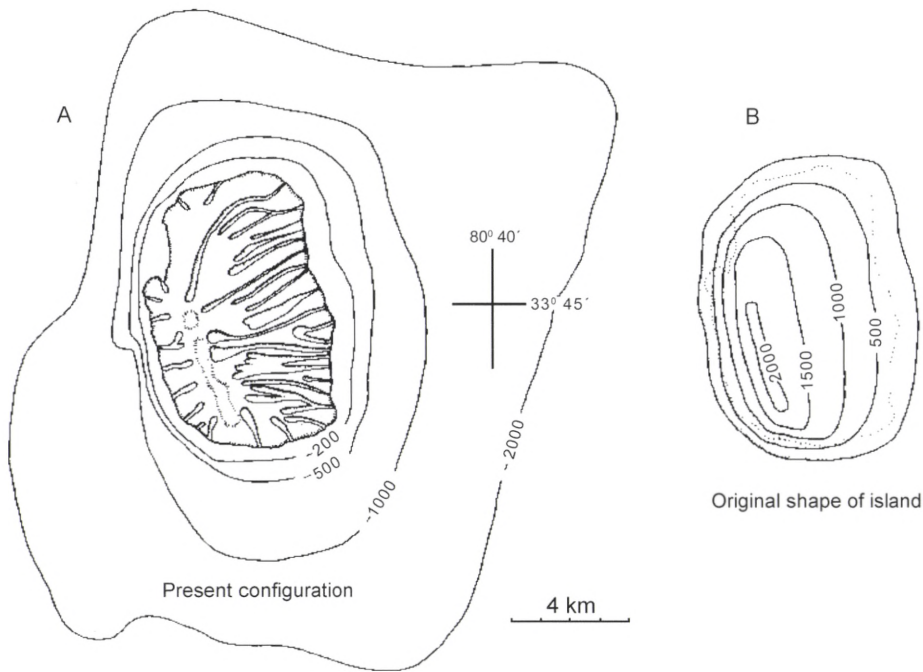
Present configuration

Original shape of island

80° 40′

33° 45′

4 km

Fig. 3. Hypothesized subsidence and erosion on Masafuera during the past one-two million years. A, present configuration of island; B, estimated shape of original island. From Sanders *et al.* (1987).
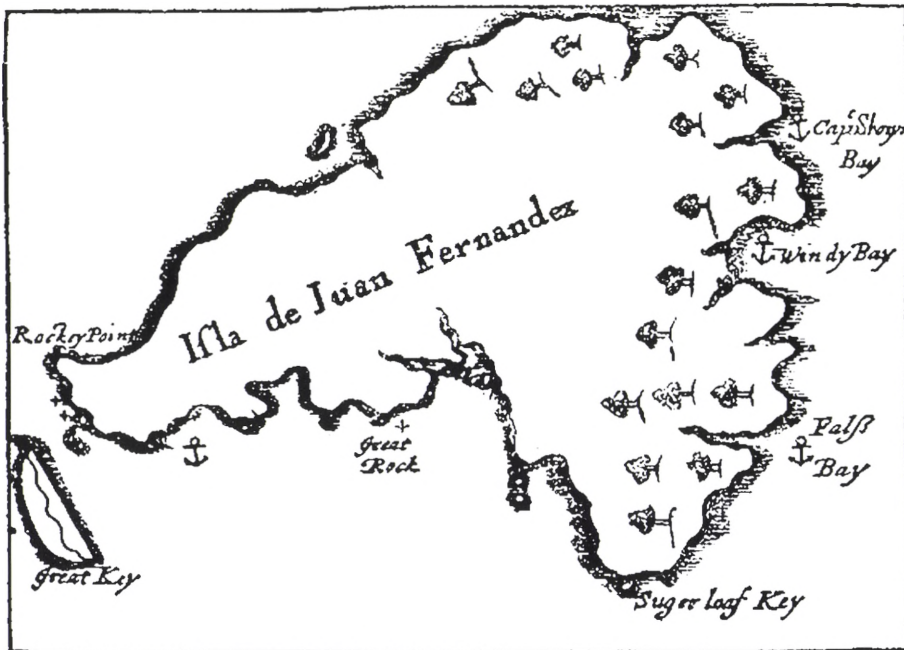

Fig. 4. Early historical map of Masatierra by Ringrose (1685).

Fewer ecological zones and populations would presumably have been lost on this island in contrast to Masatierra.

Human impacts on the Juan Fernandez Islands

It has sometimes been assumed that human island societies were perfectly integrated in their ecosystems, so that their presence did not alter the natural equilibrium of the island (for review see Kirch & Hunt 1997). Recent historical research shows a different picture (*e.g.*, see contributions in Kirch & Hunt 1997). Human arrival on islands has always been an alien intervention often of dramatic proportions with serious negative consequences for the native flora and fauna. Human arrival in Hawaii, for example, about 1000 BP, is correlated with a lasting vegetation change (Athens 1997). According to pollen diagrams, the native forests of the lowlands disappeared in a few centuries. By AD 1400-1500 there was essentially nothing left. *Pritchardia* palms and *Kanaloa* (Leguminosae) disappeared, and other native trees and shrubs dwindled to negligible numbers. By the time Captain Cook arrived in Hawaii in 1778, the native lowland forest was already gone (Athens 1997).

Sustaining human life in remote oceanic islands without an agricultural economy based on introduced plants may well have been impossible in prehistorical times. Few edible plants were naturally available, and the only edible land fauna of significance included fruit bats (never having reached Hawaii, however), birds, and on some islands, lizards and turtles. Oceanic islands were certainly not a paradise when they were first settled. Agriculture requires cultivated land, and such areas on forested islands required clearing, usually by fire. Windward forests tend to regenerate quickly, whereas the more diverse, leeward dry forests regenerate much more slowly after clearing and are more susceptible to further human disturbance and alteration (Spriggs 1997). Rousseau's "homme naturel", the "noble savage" living in harmony with the environment, in contrast with "civilized man" is certainly a fiction in oceanic islands. In the history of Polynesian colonisation, with firestick farming, there has been already a strong pre-European impact on islands. With the Europeans and their descendents in the colonies (Crosby 1986), an armada of animals and plants arrived to the islands. Weeds arrived together with introduced crops, fruit plants, forage plants, and ornamentals. Domestic animals such as goats, rabbits, pigs, all accompanied by rats, became severe pests that drove many native and endemic species toward extinction.

The Juan Fernandez Islands have the advantage that no aboriginal peoples colonized them prior to their discovery by Juan Fernandez in 1574 (Anderson *et al.* 2002). The early observations on the vegetation and taxa of the archipelago, therefore, provide some clues to the original plant life prior to human intervention. Further, because the islands were strategically located to provide a safe harbor to moor ships, to provide fresh water and meat (from sea lions and abundant fish), and to provide fresh plants to cure sailors of scurvy, many sailing vessels stopped there during the 17th-19th centuries (it was also a convenient location from which to attack the Spanish colonies along the coast of South America). Many of these voyages were long ones, often around-the-world multi-year adventures, and the experiences were often published as books containing logs of the entire trip (*e.g.*, Walter 1748). Thus there is much descriptive information on the vegetation and plants of the archipelago, especially on Masatierra, which has the more favorable bay for safe anchoring of ships.

Historical documentation from voyagers to Juan Fernandez suggests that Masatierra was

completely forested on the eastern side of the island. The low western part of the island had already subsided substantially and became dry prior to human discovery. Textual references substantiate the point of extensive forests: "... the woods which cover the island ..." (Shelvocke 1726); "The northern part of this island is ... generally covered with trees" (Anson in Walter 1748). In addition to these records, several drawings also show forests (diagrammatically) with trees covering the entire eastern part of the island (*e.g.*, Ringrose 1685; Fig. 4). The detailed map by Anson (based on observations in 1741; in Walter 1748) shows the same fully forested pattern. Surveys of the historical literature also provide a view of the extent of cutting of the endemic forest species (Stuessy *et al.* 1998a). The human impact over the past four centuries, therefore, has left Masatierra (including the small island Santa Clara) with less than 20% native forest cover (Greimler *et al.* 2002b; Fig. 5).

Impacts from invasive species in the Juan Fernandez islands

At the same time that humans cut and burned the native forests in the Juan Fernandez Islands, they also deliberately and accidentally introduced exotic animals and plants. The release of goats and pigs was a sea-faring tradition, so that fresh meat would be available on return voyages (Woodward 1969). Levels of feral animals on Masatierra have been carefully estimated from historical documents by Wester (1991).

Rabbits are a huge problem now on Masatierra, and goats still abound on Masafuera (Sanders *et al.* 1982; pers. observ.).

In addition to introduced animals, many exotic plants have also been brought to the Juan Fernandez Islands and have invaded natural vegetation dramatically (Greimler *et al.* 2002a). The worst invasives have been (and still

are; Greimler *et al.* 2002b): *Acaena argentea* (Rosaceae), *Aira caryophyllea* (Poaceae), *Anthoxanthum odoratum* (Poaceae), *Aristotelia chilensis* (Elaeocarpaceae), *Avena barbata* (Poaceae), *Briza minor* (Poaceae), *Geranium core-core* (Geraniaceae), *Rubus ulmifolius* (Rosaceae), *Rumex acetosella* (Polygonaceae), and *Ugni molinae* (Myrtaceae). Three taxa of *Vulpia* (Poaceae) have also invaded large areas (Greimler *et al.* 2002a). As pointed out by Denslow (2003), these invasives have an advantage over the native and endemic taxa of oceanic islands due to the high net resource availability of the ecosystem and the poor ability of native taxa to take advantage of these resources (*i.e.*, the invasives have a more aggressive biological syndrome). In general, the picture is not a very positive one, because the existing invasive species continue to exert a pressure upon the native and endemic flora, despite gallant conservation efforts by park service personnel (CONAF). Further, the rain of exotics continues unabated due to lack of sanitation measures for incoming foodstuffs and materials to the archipelago.

The severity of pressure being brought to bear on the Juan Fernandez archipelago from invasive plant species can be further illustrated by recent studies that estimate the extent of cover possible from selected aggressive taxa (Dirnböck *et al.* 2003). *Aristotelia chilensis, e.g.*, which is disturbing enough because of the large area already covered is likely to continue to spread without efficient control. Spatial models of potential habitats of this species predict substantial increase of its present extent, which might be a matter of a few decades. Combining this impact with that of the many other noxious weedy introduced species results in a formidable pressure against numbers of populations and population sizes of the endemic flora.

Fig. 5. Map of Masatierra showing present extent of undisturbed and disturbed native forest (adapted from Greimler *et al.* 2002a).
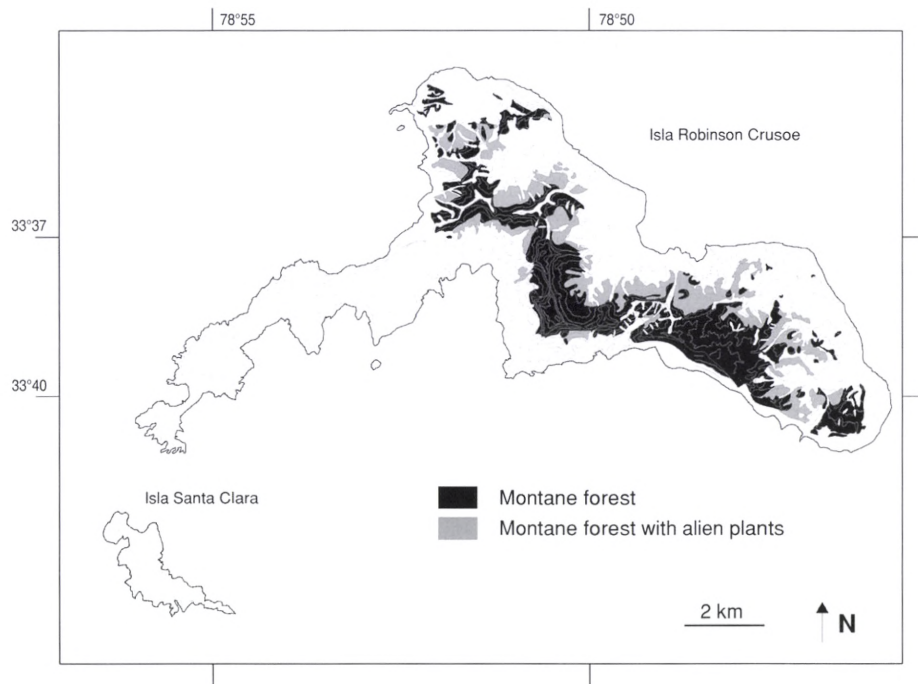
Interpreting levels of genetic variation in oceanic island plants

Because of numerous historical impacts, in many islands we are dealing with left-overs of a native and endemic flora that was much more diverse and consisted of larger populations before impacts from natural and human causes. Due to direct and indirect human intervention, many island species seem to undergo a deterministic process of reduction and extinction following exploitation, habitat destruction, and competitive exclusion from former suitable sites. Populations driven down below the minimum viable population sizes are strongly affected by demographic and environmental stochasticity. This chance variation can drive them into extinction vortices (Gilpin & Soulé 1986). In the Juan Fernandez islands, it may come as no surprise, therefore, that 21 of the endemic species in the archipelago are known to exist with no more than 25 or fewer individuals (Stuessy *et al.* 1998b).

It is in this context, therefore, that we examine the known levels of genetic variation, assayed through allozymes, in the Juan Fernandez Islands (Crawford *et al.* 2001). Twenty-nine of the endemic angiosperm species (of a total of 104, or 28%) have been analyzed. Some species show no genetic variation at all, *e.g.*, *Chenopodium sanctae-clarae*, restricted to one rock (Morro Spartan) and consisting of only one small population. Another example is the endemic monotypic family, Lactoridaceae, with *Lactoris fernandeziana*, which also shows no isozymic variation (Crawford *et al.* 1994) among the several known populations perhaps harboring a total of 1000 individuals (Stuessy *et al.* 1998c). With RAPD and InterSimple Sequence Repeats (ISSR), however, intra- and inter-populational variation can be seen (Brauner *et al.* 1992; Crawford *et al.* 2001).

Other species show considerable genetic variation, such as the widespread endemic *Myrceugenia fernandeziana* (Myrtaceae), with thousands of individuals located between 200 and 500 m, and extending up to 700 m (Greimler *et al.* 2002a; Jensen *et al.* 2002). Crawford *et al.* (2001) sought correlations with biological attributes of these endemics to explain the variation in levels of genetic variation within and among populations observed, following general life history traits reviewed earlier by Hamrick and colleagues (Hamrick *et al.* 1979, 1991; Hamrick & Godt 1989, 1996, 1997). However, Crawford *et al.* (2001, p. 2195) found: "The apportionment of genetic diversity within and among populations (G_{ST} values) is not significantly different for any of the species categories" (i.e., different life-history classes, such as differences in breeding and pollination systems, woody vs. herbaceous, etc.). The conclusion was that (p. 2202): "... one cannot make assumptions about apportionment of allozyme diversity based on pollination biology and size and distributions of populations. As emphasized by Hamrick & Godt (1996), a myriad of historical factors can shape the diversity now seen in plant species, and island endemics are especially subject to certain of these factors because of rapid and recent changes in population sizes and breeding systems (Anderson *et al.* 2001) and recent speciation."

Similar studies of allozyme variation have been done for 69 endemic species of the Canary Islands (Francisco-Ortega *et al.* 2000). Once again, based on attempts to explain observed genetic diversity within and among populations (p. 910): "These data do not indicate a consistent trend for higher diversity in outcrossing compared to selfing species." Further, in comparing relationships of related species among islands of the archipelago, they also note (p. 911): "If there were loss of variation due to drift or founder events associated with recent speciation, then the more recently

derived species would be expected to display lower alloyzme diversity than basal taxa. Clearly, this is not the case." Another noteworthy point is that, in general, the levels of varation between populations within species is twice as high as reported for such systems in Pacific Island archipelagoes (*e.g.*, in Juan Fernandez, Crawford *et al.* 2001; in Hawaii, Witter & Carr 1988). Francisco-Ortega *et al.* (2000) also focus on historical factors, including the greater age of some of the islands in the Canarian archipelago (the oldest being Fuerteventura with an age of more than 21 million years; Carracedo 1984, 1994).

A more direct comparison to reveal genetic founder effects would be to compare levels of genetic variation in progenitor and derivative species in continental and oceanic island habitats. Only two examples are known to us: in *Rhaphithamnus* (Verbenaceae, Juan Fernandez Islands, Crawford *et al.* 1993) and in *Gossypium* (Malvaceae, Galapagos Islands, Wendel & Percival 1990). In the former, there are only two known species, *R. spinosus*, restricted to low elevations in the southern Andes, and *R. venustus*, endemic to both islands of Juan Fernandez. In this instance, a dramatic reduction in genetic variation among populations was noted in the island endemic, in fact, among the 14 populations analyzed, the variation was one-fourth that seen in two populations of the mainland species. Further, the island species is gynodioecious, and hence promoting outcrossing, in contrast to the hermaphroditic mainland species. The difficulty in this case is how to interpret this as a result of a founder event. Neither species occur in large populations, but in the island the individuals occur in lower density than in the continent. In any event, due to the massive alteration of the landscape, especially on Masatierra (the island best documented for vegetation alteration), it is simply impossible to be certain that the low level of genetic diversity encountered reflects a

founder event or simply loss of variation through time due to habitat reduction.

The second example of comparing a continental progenitor and derivative oceanic island species is in *Gossypium* (Wendel & Percival 1990), with *G. klotschianum* endemic to the Galapagos Islands and *G. davidsonii* from Baja California, Mexico. Results show higher interpopulation genetic variation in allozyme loci for the Mexican species in contrast to less variation in the Galapagos endemic (*e.g.*, number of alleles per polymorphic locus, 1.85 vs. 1.31, respectively, and inter-population genetic identities 0.917 vs 0.987). Data suggest that the derivative species originated recently "… and that it suffered a severe genetic bottleneck as a consequence of a founding event." (p. 110). Again, it is difficult to separate this hypothesis from that of reduction in population number and size as a result of historical impacts, both natural and human-induced, that have also occurred in the Galapagos Islands (*e.g.*, Cox 1983; Hamann 1984).

Conclusion

The main point of this paper is to urge caution in interpreting reasons for levels of presently observed genetic variation in endemic species of oceanic archipelagoes. Understanding the reasons for observed genetic variation demands a synthesis of biological and historical factors. Oceanic islands have long been regarded as models for evidence of founder effects, simply because the probability of propagules arriving and establishing in far-away small land masses must, through simple common sense, be limiting the genetic breadth of the founder population in comparison with continental source regions. New molecular markers have now provided means for directly measuring levels of genetic variation in island systems, and often reduced genetic variation is seen in island endemics (Frankham 1997). The evolutionary significance of this observation, however, in terms of understanding plant speciation in oceanic islands, is by itself unclear. A variety of historical impacts have acted on these populations. Further, there is some indication that not all island endemics are as genetically depauperate as one might think. Genetic variation perhaps accumulated after the founder event of early colonization through mutation and recombination in the first million years (*e.g.*, as seen in Ullung Island, Korea; M. Pfosser & T. Stuessy, unpubl.). Such initial populational build-up might, in fact, support adaptive morphological variation in response to different habitats in oceanic islands. This, however, might be followed by population decline and reduction in genetic variation through time as the various historical factors act upon the island biota. What is needed are direct observations of newly arrived populations of native species in newly created natural islands, such as with the origin of Surtsey several decades ago (Fridriksson 1975) off the coast of Iceland.

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