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Tod F. Stuessy  
*Institut für Botanik*

Ulf Swenson  
*Uppsala University*

Daniel J. Crawford  
*Ohio State University*

Gregory Anderson  
*The University of Connecticut, Storrs*

Mario Silva O.  
*Universidad de Concepcion*

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## PLANT CONSERVATION IN THE JUAN FERNANDEZ ARCHIPELAGO, CHILE

TOD F. STUESSY

*Institut für Botanik  
Universität Wien, Rennweg 14, A-1030  
Vienna, Austria*

ULF SWENSON

*Department of Systematic Botany  
Uppsala University, Uppsala 752 36, Sweden*

DANIEL J. CRAWFORD

*Department of Plant Biology  
Ohio State University, Columbus, Ohio 43210*

GREGORY ANDERSON

*Department of Ecology and Evolutionary Biology  
The University of Connecticut, Storrs, Connecticut 06269*

AND

MARIO SILVA O.

*Departamento de Botanica  
Universidad de Concepción, Concepción, Chile*

### ABSTRACT

Oceanic archipelagos often hold very specialized floras with high degrees of endemism. These floras are frequently highly vulnerable to disturbance by natural causes and human intervention. The Juan Fernandez Islands (Chile) in the Pacific Ocean are a small archipelago of only three islands. Since discovery in 1574 by Juan Fernandez, human activities have altered floristic composition and survival circumstances of the endemic species. In this paper we document past and present means of disturbance, both anthropogenic and natural, which have influenced the native vegetation. The most destructive past activities have been logging and introduction of animals and plants, both deliberately and inadvertently. At the present time, exotic organisms are still introduced as pets, ornaments, or for soil conservation. All pose serious threats to the natural vegetation as shown by altered floristic composition, populational decline of endemic taxa, and even extinction. Weeds that form impenetrable thickets are *Aristotelia chilensis*, *Rubus ulmifolius*, and *Ugni molinae*. Recent introductions include the aggressive *Lantana camara* and *Lonicera japonica*. Examples of endemic taxa in need of conservation are *Dendroseris*, *Lactoris*, and *Robinsonia*. Previous studies reveal that island taxa frequently have low levels of genetic variation, a pattern also seen in many endemic taxa of the Juan Fernandez Islands. Conservation programs are urgently needed that emphasize physical and biological measures for controlling alien weeds and animals.

Key words: conservation, exotic organisms, *Dendroseris*, Juan Fernandez, *Lactoris*, *Robinsonia*, weeds.

### INTRODUCTION

Oceanic islands are natural laboratories for the study of plant evolution. Because of their small size and well-circumscribed ecological systems, islands can often show more precisely the results of evolutionary phenomena, especially through studies of endemic taxa. Concepts such as adaptive radiation have been developed in more detail in oceanic archipelagos (e.g.,

Carlquist 1965, 1974). The time dimension for evolutionary events is also measurable more precisely than in most continental regions due to dating the sequences of island volcanism. For endemic taxa, patterns of phylogeny may also be interpreted with a high degree of confidence because of the known time frame. In addition, equilibrium theories of island biogeography (e.g., MacArthur and Wilson 1967) have addressed basic questions of immigration and extinc-

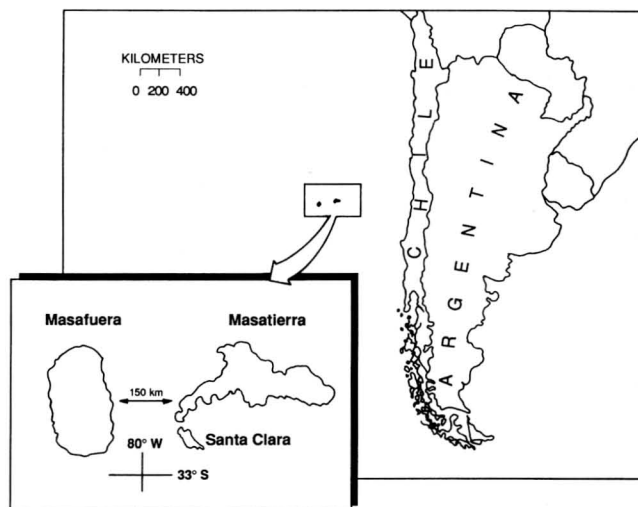


Fig. 1. Map showing the location of the Juan Fernandez Islands, Chile.

tion of island biota. These studies offer insights not only for basic ecological and biogeographic phenomena, but also for proper management of natural resources and natural preserves (e.g., Simberloff and Abele 1982; Harris 1984; Swenson et al. 1997).

Many endemic species exist in floras of oceanic islands, and often some of these are extremely rare. Many pressures exist on the survival of rare species, including natural forces such as erosion, predation, and disease. But most important have been human activities such as developments for housing and roads, the introduction of domesticated animals, and the establishment of feral animals in various parts of the natural environment. Further, many weeds have been introduced that have placed additional pressures on preservation of the native flora. A great need exists, therefore, for immediate conservation measures to preserve the biodiversity, genetic resources, and unique aspects of island biota so that they can be utilized not only for evolutionary studies but also for possible ethnobotanical, medicinal, ornamental, and other economic potentials. One such group of islands with high endemism are the Juan Fernandez Islands (Chile).

The Juan Fernandez archipelago (Fig. 1) lies 580 to 730 km west of the Chilean coast and consists of three islands: Masatierra and Santa Clara in the east ( $33^{\circ}37'S$ ,  $78^{\circ}50'W$ ) and Masafuera in the west ( $33^{\circ}45'S$ ,  $80^{\circ}46'W$ ). Masatierra and Masafuera are known to be approximately four and one-two million years old, respectively (Stuessy et al. 1984a). All islands cover a surface of  $100.2 \text{ km}^2$  (Stuessy 1995) of which Masafuera ( $50 \text{ km}^2$ ) is slightly bigger than Masatierra ( $48 \text{ km}^2$ ).

The Juan Fernandez Islands were declared a National Park in 1935 and a Biosphere Reserve in 1977 (Wester 1991). A management plan was set up and published in 1976 (Anonymous 1976). Most of the

three islands are included in the park except the village of San Juan Bautista on Masatierra, the only permanent settlement in the archipelago.

Endemism in the Juan Fernandez Islands is high relative to age and area of the archipelago. First, the monotypic paleoherb family Lactoridaceae has found its only refugium here, growing on the high ridges of Masatierra (Skottsberg 1953). Second, according to Stuessy et al. (1992) there are 158 extant flowering plant species in the islands, of which ca. 100 are endemic. If the ferns are included, another 23 endemic species are added. This gives a level of endemism of 60% for vascular plant species, 11% for genera, and one endemic family.

Many taxonomic and evolutionary studies have already been completed on the endemic flora. The first flora was published by Johow in 1896. In the 1900s, Carl Skottsberg made a series of expeditions. Subsequent studies provided a detailed description of the floristic elements of the archipelago and laid a strong foundation for additional investigations (Skottsberg 1921, 1951, 1953). Further, Skottsberg (1956) synthesized available information on the phytogeography of the islands. Subsequent studies have included, for example, a recent vegetation analysis by Schwaar (1979) focusing on transect studies on one major peak on Masatierra, and the vegetational and floristic summary by Hoffmann and Marticorena (1987).

As a result of evolutionary and systematic interests in the flora of the Juan Fernandez Islands, detailed studies during the past decade have been pursued by the Departments of Botany of the Ohio State University (USA) and the Universidad de Concepción, Chile. The objectives of this collaborative research have been (1) to examine the native species for chemical compounds, their identity, medicinal, and therapeutic value; (2) to understand the patterns and processes of evolution in the endemic vascular flora; and (3) to produce a modern flora of the vascular plants. The second objective is sufficiently broad to be subdivided into four subareas of which a number of studies are completed. This includes studies on karyomorphology and embryology (Sanders et al. 1983; Spooner et al. 1987; Sun et al. 1990; Tobe et al. 1993); levels of genetic variation within and among populations (e.g., Crawford et al. 1990, 1992b, 1994; Brauner et al. 1992); modes and patterns of speciation (e.g., Sanders et al. 1987; Stuessy et al. 1990; Crawford et al. 1992a; Sang et al. 1994); and biogeography with emphasis on plausible source areas and/or biogeographic connections (Stuessy et al. 1990; Valdebenito et al. 1990).

In terms of conservation, the endemic flora of the Juan Fernandez Islands needs great attention. Skottsberg (1921) earlier expressed his concern regarding how fragile the flora might be. Since then, floristic changes have clearly taken place as shown by Sanders

et al. (1982). The diversity of species in the archipelago is being reduced through human activities, and especially from feral animals and introduced weeds. These factors enhance the rapid erosion of the volcanic soil, which in turn offers preferential survival opportunities for weedy species. The number of weeds is still increasing; about 190 taxa were reported in 1993 (Matthei et al. 1993), and now, only three years later, 227 alien taxa are known (Swenson et al. 1997), making up 52% of the total vascular flora of the archipelago.

The purposes of this contribution are to (1) indicate the existing natural and anthropogenic pressures on the natural vegetation of the Juan Fernandez Islands; (2) discuss selected endemic species that are truly in need of conservation at this time; (3) mention the degree of genetic resources available to some endangered taxa; and (4) recommend procedures for conservation.

#### PRESSURES ON THE NATURAL VEGETATION

Natural factors can bring about plant extinction on volcanic islands. Erosion is intense with friable volcanic soils easily fragmented by wind, water, and biotic activity. Frost action is minimal in the Juan Fernandez Islands. There are verbal accounts of snow at the top of Masafuera, but this is a rare occurrence. The most severe, long-term loss of surface area results from subsidence of the islands as the Nazca Plate creeps eastward and subducts under the South American continent (González-Ferrán 1987). Thus, erosion and subsidence slowly and inexorably alter the available space for organisms. Sanders et al. (1987) reconstructed the geological history of Masatierra, including its surface area, altitude, and meteorological factors, based on bathymetric contours. They hypothesized that Masatierra was about 3,000 m high and possibly 20 times larger when it was formed approximately four million years ago. Hence, Masatierra may have held many more taxa than present today. In other words, Masatierra during the past three–four million years has probably lost 95% of its original surface area, 2,000 m in altitude, and many environments due to erosion and subsidence. One may suspect that many endemic species might also have disappeared during this time. It is impossible to know for certain, but a 25–50% loss of total vascular species would seem likely. Southwestern Masatierra, for example, is presently extremely dry, with few native taxa, and may illustrate this process. The area is desertlike and the vegetation is very sparse, most probably not due to human impact; early chronicles of the island suggest that this sector was already dry by the time people visited in the 17th century (e.g., Ringrose 1685).

#### Humans

Activities by humans have provided by far the greatest pressures on the flora, including acceleration of erosion. Because the position of the archipelago represented a convenient stopping place in past centuries for ships to replenish firewood and conduct repairs, the native forest trees were soon depleted at lower elevations, especially on Masatierra (e.g., Gay 1854). These practices left a number of areas without any good ground cover and subsequent erosion has set in. The eastern part of Masatierra, above Puerto Francés, was apparently severely logged during the 18th and 19th centuries, and is now completely denuded with little soil or vegetation; only bare lava rock remains (Fig. 2).

Fire is another factor influencing natural vegetation on the archipelago. Natural fires from lightening must occur, but it is not known how frequent these are, or have been. Certainly, fires set by human carelessness do happen and have been documented (Woodward 1969). In fact, as recent as February 1996, 70 hectares burned as a result of an apparently accidental fire set by fisherman on Masafuera (Barría 1996).

San Juan Bautista on Masatierra, the only permanent settlement, has about 500 inhabitants (Hernández and Monleon 1975). Masafuera is uninhabited except for a community of 15 lobster fisherman and their families, who stay there about eight months of the year. The park administration (Corporación Nacional Forestal, or CONAF) estimates that approximately 1000–1400 tourists come annually to the archipelago (pers. comm.). Masatierra receives most of the traffic by air and by boat, including a monthly supply ship. An insignificant number visit Masafuera.

#### Domesticated Animals

In addition to cutting of native forests, humans have contributed in other negative ways by domesticated and feral animals, which have been allowed to roam freely and reproduce on both islands. Cows, donkeys, horses, pigs, rabbits, and sheep are all introduced (e.g., Hoffmann and Marticorena 1987; Wester 1991) and penetrate the forests throughout Masatierra and Masafuera. Goats and rabbits have been and still are a major problem. On Masatierra, the goat population is down to about 50 animals due to continuous hunting, but the rabbit population is estimated to be at least 5000 animals (B. López, pers. comm.), causing a severe pressure on the natural vegetation. In contrast, feral animals on Masafuera are more conspicuously problematic with some 5000 goats (B. López, pers. comm.). These have had a tremendous impact on the endemic flora. The coati mundi (*Nasua nasua*) is another exotic animal, which originally was introduced as a pet but has escaped from captivity, reproduces on





Fig. 2. Badly eroded area near Puerto Francés on Masatierra, Juan Fernandez Islands.

Masatierra (pers. observ.) and disturbs the soils, which accelerates erosion during spring rains. Introduced rats, abundant on Masafuera (Hoffmann and Marticorena 1987), also cause damage due to their omnivorous diet.

#### Exotic Plants

Few ecological studies have been conducted to understand the changing floristic composition of the vascular flora. Two previous authors, Johow (1896) and Skottsberg (1953), are the only reliable historical sources available. Sanders et al. (1982) used these in conjunction with new observations to point out that a loss of diversity has occurred and a number of endemic species are thus in need of conservation. The general trend is for more weeds on Masatierra, which is more frequented by boats, airplanes, and tourists. Masafuera shows a drop in native species diversity, probably due to pressure by feral animals, but a smaller increase in introduced weeds (Sanders et al. 1982).

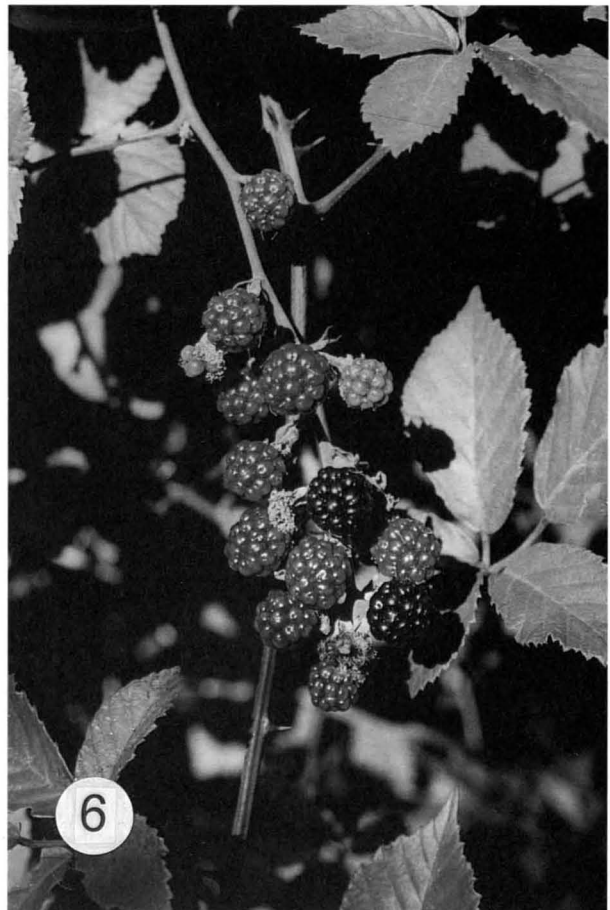
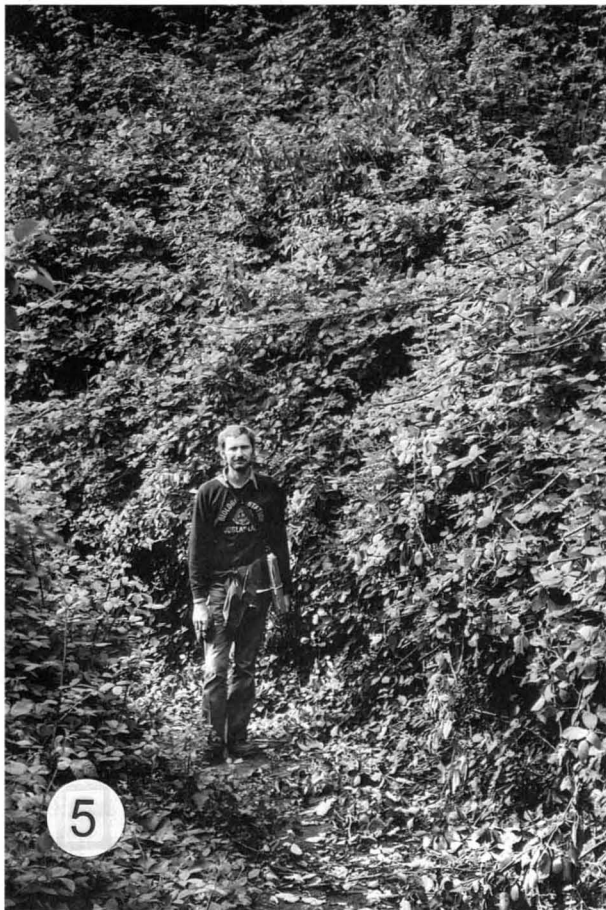
Exotic plants are not emphasized as often as introduced animals for threatening the natural vegetation. Only a few exotic plants were observed by Mary Graham, who, in 1823, was the first botanist to visit Masatierra. From this date until 1996, more than one exotic

species on average has been added annually, resulting in 227 out of 436 species (Swenson et al. 1997). Some of the exotic species (more than 13) have become extremely serious plagues in need of attention. These include *Acaena argentea* Ruiz et Pavon (Rosaceae), *Anthoxanthum odoratum* L. (Poaceae), macqui, *Aristotelia chilensis* (Molina) Stuntz (Elaeocarpaceae, Fig. 3, 4), *Conium maculatum* L. (Apiaceae), zarzamora, *Rubus ulmifolius* Schott (Rosaceae, Fig. 5, 6), and *Ugni molinae* Turz (Myrtaceae). Except *Anthoxanthum* and *Conium*, all are shrubby species with fleshy, bird-dispersed fruits, with tremendous reproductive capacities, and competitive abilities in virtually any situation. All of them cover large fields of many acres on both Masatierra and Masafuera. These species, especially *Aristotelia* and *Rubus*, form impenetrable thickets which prohibit native species from growing beneath (Fig. 3, 5). Further, they are extremely aggressive weeds, colonizing open soil and eroded habitats on which native species cannot successfully grow or compete.

Swenson et al. (1997) reported 40 new records of alien taxa for the Juan Fernandez Islands, of which 36 species appeared on Masatierra. Among these are some well-known worldwide, noxious shrubby weeds, such as *Ipomoea indica* (Burm.) Merr. (Convolvula-

→

Fig. 3–6. Serious weeds on the Juan Fernandez Islands.—3. Dense stand of *Aristotelia chilensis*.—4. Fruiting branch of *Aristotelia chilensis*.—5. Impenetrable thickets of *Rubus ulmifolius*.—6. Branch of *Rubus ulmifolius*, showing prickles.



ceae), *Lantana camara* L. (Verbenaceae), and *Lonicera japonica* Thunb. (Caprifoliaceae). So far, none of these species has yet invaded into the National Park, but immediate measures are needed to prevent their intrusion into natural vegetation. As pointed out by many authors, the latter two cause extensive problems in both disturbed and undisturbed habitats (e.g., Lawesson and Ortiz 1990, and references therein; Wagner et al. 1990). *Ipomoea indica*, a twining herbaceous to somewhat woody vine with large, attractive flowers sets fruit as dry capsules. Its means of dispersal is not clear, but this taxon is very abundant in disturbed areas in San Juan Bautista and will no doubt extend its range. *Lantana camara* was found exclusively in gardens, but this extremely dangerous pest has caused much trouble worldwide. For example, on Hawaii it has invaded natural forests (Wagner et al. 1990) and in the Galapagos Islands it has put several endemic plants at the rim of extinction plus threatening breeding sites of birds (Cruz et al. 1986). *Lonicera japonica*, a trailing vine and also a troublesome weed, was reported as naturalized in the Juan Fernandez Islands (Swenson et al. 1997). *Lonicera* and *Lantana* both have fleshy fruits, like *Aristotelia*, *Rubus*, and *Ugni*, and thus have potential of being dispersed into the native vegetation in the near future.

*Acaena argentea* has been present since 1864 on Masatierra and since 1916 on Masafuera (Matthei et al. 1993). It already was abundant at the turn of the century and Johow (1896) cited it as a problematic weed, covering pastures, and turning them into unproductive land. Johow stated that the only places free from *A. argentea* were virgin forests. The full range of *Acaena* is not known but individuals and small pockets are even found on precipitous slopes dominated by *Ugni molinae*. One example must be mentioned: the lower part of Corrales de Molina on south-central Masatierra is completely covered by *A. argentea*.

*Anthoxanthum odoratum* was first collected on Masatierra and Masafuera in 1869 (Matthei et al. 1993). On Masafuera it was abundant in deforested areas by the 1890s (Johow 1896). Sanders et al. (1982) mentioned it as occurring more frequently than in Skottsberg's study in 1953. It is now very common on both islands, from sea level to the highest peaks, perhaps the most abundant grass on both Masatierra (pers. observ.) and on Masafuera (Skottsberg 1921).

*Aristotelia chilensis* (Fig. 3, 4) was first collected on Masatierra in 1864 and on Masafuera in 1916 (Matthei et al. 1993). In 1896, Johow reported that the species already was as a troublesome weed. On Masatierra, Skottsberg (1953) noted *Aristotelia* in almost all valleys, on slopes, in the native forests, and occasionally in the higher areas. According to Skottsberg (1953), the native vegetation would "gradually transform"

into *Aristotelia* stands, because it simply prevents native species from germinating under it. The species has continued to spread up the ridges and into virgin vegetation (Sanders et al. 1982, pers. observ.). On Masafuera, *Aristotelia* was reported as scarce (Skottsberg 1953) and is still less common today—perhaps eaten by the numerous goats?

*Conium maculatum* was first collected in 1984 on both Masatierra and Masafuera (Matthei et al. 1993). It often grows in very dense thickets in eroded areas, excluding other vegetation except the dangerous weed, *Acaena argentea*. Thick patches have been observed by us on Masatierra, for example, in Valle Francés, at the top of La Piña (ridge), at the sea front in San Juan Bautista, in the valley La Vaquería, and on Masafuera in Quebrada Casas.

The first collections of *Rubus ulmifolius* from Masatierra and Masafuera are, respectively, from 1927 and 1965 (Matthei et al. 1993). Looser (1927), who first reported the species, commented that this introduction was most regrettable. It was possibly introduced for use as living corrals (Oehrens and Garrido 1986) and for food. It has become one of the (if not *the* most) noxious weeds in the archipelago. Skottsberg (1951) ranked the species as an "extremely dangerous weed." Sanders et al. (1982) reported impenetrable undergrowth of *R. ulmifolius* and regarded it as an especially dangerous weed due to its rapid vegetative growth (Fig. 5–6) and bird-dispersed fruits. For more than 15 years we have confirmed Skottsberg's prediction. *Rubus ulmifolius* continues to extend its range, primarily in disturbed areas, but also is expanding into virgin forests. By scrambling upon other vegetation it simply takes over acre after acre and drastically changes the floristic composition. For example, valley Colonial, below El Yunque and above San Juan Bautista, is literally covered with *R. ulmifolius*. Biological control of this species, however, may be feasible as shown by Oehrens and Garrido (1986), using the specific rust fungus *Phragmidium violaceum* (Schultz) G. Winter. Systemic poisons may also be recommended after careful ecological study.

*Ugni molinae* was first collected on Masatierra in 1892 (Matthei et al. 1993). The exact year of introduction is unclear, but the plant was most likely deliberately introduced for its edible aromatic fruits. In the 1890s, it was restricted to the valley up from Cumberland Bay and along the trail toward Mirador Selkirk (Johow 1896). In 1917, *U. molinae* still had not extensively spread (Skottsberg 1953). Since this time, however, the species has spread enormously over the entire island, up the knife-edged ridges, down adjacent slopes, and into neighboring valleys. In contrast to this, the congeneric endemic species *U. selkirkii* (Hook. et Arn.) O. Berg was abundant on the ridges above Cumberland Bay in the beginning of the 1900s



(Skottsberg 1953). Today, however, *U. selkirkii* is almost completely replaced by *U. molinae* and only found occasionally above 500 m. *Ugni molinae* also is now regrettably present on Masafuera (Matthei 1995).

### Hybridization

Hybridization is another threat to endemic taxa on oceanic islands. Because of rapid speciation, few genetic barriers often separate congeneric species (e.g., Crawford et al. 1992b), and hence interspecific and intergeneric hybridization if it becomes extensive can reduce species diversity. Pacheco et al. (1991) showed that natural interspecific hybridization occurs between two endemic species of *Gunnera* L. in the archipelago. They concluded that disturbance of natural habitats was the likely factor that promoted this hybridization.

Another example of hybridization is  $\times$ *Margyracena skottsbergii* Bitter (in Skottsberg 1921). The plant was a putative intergeneric hybrid between the introduced weed *Acaena argentea* and the endemic species *Margyricarpus digynus* (Bitter) Skottsb. This hypothesis was confirmed using random amplified polymorphic DNA (RAPD) as markers (Crawford et al. 1993a). *Margyricarpus* was once a common species on Masatierra (Skottsberg 1921) but has not been found during the past 20 years despite extensive fieldwork. Apparently, *A. argentea* has excluded the endemic species.

### CRITICAL SPECIES IN SPECIAL NEED OF CONSERVATION

The approach here is to highlight some of the species in need of special attention for conservation. There are more species that could be mentioned, but the examples given are indicative of the need for conservation if these and other taxa are to be preserved for future generations.

### Extinct

We know that one species has gone extinct during historical time: the endemic sandalwood, *Santalum fernandezianum* F. Phil. Sandalwood was much appreciated and sold for its aromatic wood to oriental markets (Woodward 1969). As Skottsberg (1953) postulated, sandalwood was probably quite common until "reckless exploitation" began in the 19th century. Skottsberg (1910) managed to photograph the last living individual of the species on Masatierra in 1908. In 1916, this last plant had died and pieces were cut up and sold (Hoffmann and Marticorena 1987). Pieces were still in circulation in 1996, perhaps from this very last tree. From herbarium material, wood pieces, and geographic names (Quebrada del Sándalo), we know that sandalwood grew on both Masatierra and Masafuera, but lack of herbarium material from Masafuera

precludes knowing if one or two vicariant species existed (Skottsberg 1953).

### Saved from extinction

Two species, *Chenopodium sanctae-clarae* Johow and *Dendroseris litoralis* Skottsb., are for the present saved from extinction. *Dendroseris litoralis* is known in the wild (Skottsberg 1953) only from two small rocks along the coast of Masatierra (Morro Viñillo) and Santa Clara (Morro Spartan). *Chenopodium sanctae-clarae* is a local endemic on Santa Clara, but due to the impact of goats its last refugium is now restricted to Morro Spartan (Skottsberg 1953; Stuessy et al. 1992), where 58 individuals persisted in the 1980s (Stuessy et al. 1984b). Both species were brought to CONAF's garden on Masatierra and successfully propagated. *Dendroseris litoralis* now occurs almost in every garden on the island, along the streets of San Juan Bautista, as an ornamental in continental Chile, and in several botanical gardens around the world. It has adapted well to cultivation and there is no reason to believe that it will become extinct in the future. Likewise on Masatierra, *Chenopodium sanctae-clarae* in the past few years has been found in gardens, often as a robust, well-grown, and easily shaped hedge plant. It is even reported as naturalized on Masatierra (Swenson et al. 1997).

### Endangered Species

One can focus on endangered species in the Juan Fernandez Islands based on numbers of individuals and taxonomic level. In this context, paramount significance should be the monotypic paleoherb family Lactoridaceae, composed of *Lactoris fernandeziana* Phil. (Fig. 7). Next in priority would be all the endemic genera, i.e., *Centaurodendron* Johow, *Cuminia* Colla, *Dendroseris* D. Don, *Juania* (Mart.) Drude ex Hook.f., *Megalachne* Steud., *Podophorus* Phil., *Robinsonia* DC., *Selkirkia* Hemsl., *Thyrsopteris* Kunze, and *Yunquea* Skottsb. The last group to be mentioned would be endemic species, which represent larger genera of broad subtropical and/or temperate distribution. All these taxa, however, are important for conservation.

*Lactoris fernandeziana* survives refugially on Masatierra. Based on fossil pollen it represents a family about 90 million years old (Zavada and Benson 1987). The evolutionary relationships of this shrubby family are still debated. Some suggest that it is distantly allied to other families in the Magnoliales (Crawford et al. 1986; Lammers et al. 1986); others emphasize a placement in, or near, the Piperales based on wood anatomy and embryology (Carlquist 1990; Tobe et al. 1993), and more recent cladistic analyses using morphology or molecular data sets suggest affinity to Aristolochi-



Fig. 7. Endangered family of the Juan Fernandez Islands, the monotypic Lactoridaceae (*Lactoris fernandeziana*).

ales (e.g., Qiu et al. 1993; Doyle 1994). For a long time this taxon was regarded as the most endangered species of them all in the Juan Fernandez Islands, possibly even extinct (see Lammers et al. 1986). Lammers et al. (1986) located six individuals in five sites. Later expeditions in 1990 and 1991 of Ohio State University-Universidad de Concepción, revealed that 1000 or even more individuals are extant (Crawford et al. 1994). But still, *Lactoris* is restricted to Masatierra and the fog swept mountain forests on the very high, knife-edged ridges at 500 m and above, and therefore must be regarded as rare. *Lactoris* is cultivated in CONAF's garden and the Royal Botanic Gardens, Kew, the latter having been successful just recently (pers. observ.). In our laboratories, we obtained successful germination of *Lactoris* seeds, but only two seedlings developed to 5–120 cm tall and finally perished of unknown causes. Tissue culture may provide an avenue for improved cultivation. For the time being, with possibly 1000 individuals in the wild, conservation of *Lactoris* may not seem a high priority. However, its distribution is limited, and the introduced *Ugni molinae* is invading ridges to their very tops and down the other side. It would be important, therefore, to investigate measures to reduce the expansion of *U. molinae* and to protect the habitat in which *Lactoris* still thrives.

Asteraceae are the largest plant family of the archipelago. Many genera of this family have evolved the tree-habit: *Dendroseris* with eleven species (Fig. 8),

*Robinsonia* with seven species (Fig. 9), *Centaurodendron* with two species, and the monotypic genus *Yunquea* (Bremer 1994). These are all endemic and most of them are extremely scarce.

Species of *Dendroseris* (Lactuceae) exist in different degrees of rarity. *Dendroseris litoralis* survives from only a few plants in the wild, but it proliferates in cultivation (see above). A close relative, *Dendroseris macrantha* (Bertero ex Decne.) Skottsb., however, is nearly extinct. One plant was found by us on an expedition to Masatierra in 1980, in a garden in San Juan Bautista, later cut down and now apparently gone. Another plant has been found in the wild and a single immature individual now grows in CONAF's garden. *Dendroseris regia* Skottsb. is only known from Masafuera, growing mainly above 900 m. Ricci (1995) reported more than 100 individuals of this taxon but they are still rarely found in flowering condition and propagation has been unsuccessful. *Dendroseris neriifolia* (Decne.) Hook et Arn. (Fig. 8) is known only from three large plants on the path from Pangal to Puerto Francés. However, as with *D. litoralis*, *D. neriifolia* has been taken into cultivation in CONAF's garden, as well as in the botanical garden of Viña del Mar (Ricci 1995), and hence has good potential for survival.

The dioecious genus *Robinsonia* belongs in tribe Senecioneae and is the second largest genus in the archipelago. All species, except *R. masafuerae* Skottsb., are restricted to Masatierra. They are scattered on the





Fig. 8–9. Representatives of the endangered flora of the Juan Fernandez Islands.—8. *Dendroseris neriifolia* (Asteraceae).—9. The dioecious genus *Robinsonia* (Asteraceae), represented by a female (left) and a male individual (right) of *R. gracilis*.

high ridges where most of them survive well. The conspicuous exceptions, however, are *Robinsonia macrocephala* Decne., which has not been seen in recent years and is possibly extinct. *Robinsonia berteroi* (DC.) Sanders, Stuessy et Marticorena is a problem,

as only one plant is known and it is staminate. No species of the genus is presently in cultivation.

A third genus, *Centaurodendron*, has two species restricted to the high ridges on Masatierra and both are extremely scarce. The “dark blue” flowers of *C. dra-*

*caenoides* Johow were first seen in 1953 (Skottsberg 1953), photographed in 1986 by M. Brooke (copy with T. Stuessy) as "pink", and according to our knowledge never seen again. Flowers of the even rarer *C. palmiforme* Skottsb. have never been found by us in spite of extensive field work. The related monotypic *Yunquea* grows only at the top of the tallest peak on Masatierra, El Yunque, at about 900 m. This plant has never been collected by professional botanists and its present status is uncertain.

#### Rare Endemic Species

Many endangered endemic species occur in larger genera with broad subtropical and/or temperate distributions. On Masatierra examples could include three species of *Eryngium* L., *Peperomia margaritifera* Bert. ex Hook., and *Plantago fernandeziana* Bert ex Barnéoud. *Eryngium bupleuroides* Hook. et Arn., *E. fernandezianum* Skottsb., and *E. inaccessum* Skottsb. are all scarce with the latter two more so than the former. These are truly woody species, one of which is presently in cultivation. It has been suggested that *E. fernandezianum* might be a hybrid between the other two taxa (Skottsberg 1921). More studies are needed to test this hypothesis. *Peperomia margaritifera* is confined to one small area of Masatierra and cultivation is highly recommended. This should not be too difficult, as the genus is well adapted for greenhouse survival. *Plantago fernandeziana*, with its woody base, is a tree-like member of a normally herbaceous genus and is found only above 430 m on Masatierra's highest ridges. The species is in extreme danger of extinction. A few individuals are presently grown in CONAF's garden but broader scale cultivation would be appropriate.

Examples of endangered species on Masafuera include *Ranunculus caprarum* Skottsb. and *Berberis masafuerana* Skottsb. The former is extremely rare and is now only found in the highest and most secluded regions where pressure from feral goats is low. *Berberis masafuerana* was initially described by Skottsberg (1921) from vegetative material. Flowers and fruits are still poorly known and the first fruit ever discovered was found by us in 1986.

#### GENETIC RESOURCES IN THE ENDANGERED FLORA

Previous studies of genetic resources have often shown low genetic diversity. For example, Lowrey and Crawford (1985) discovered very little genetic divergence among species of *Tetramolopium* Ness (Asteraceae), a genus thought to have reached the Hawaiian islands by a single introduction from New Guinea. Likewise, very little genetic differentiation was found among related species of *Bidens* L. (Asteraceae: Helenurm and Ganders 1985). Studies by Witter and Carr (1988) in *Dubautia* Gaudich., also in Asteraceae, have

shown that species occurring on older islands in the Hawaiian archipelago exhibit lower genetic similarities than taxa inhabiting younger islands. In other words, presumptive older species show higher genetic divergence than younger ones although they perhaps all had a single ancestor.

Six studies have been conducted of Juan Fernandez endemic taxa to determine the amount of variation at isozyme loci within natural populations. Results from five of those analyses, *Chenopodium* (Crawford et al. 1988), *Dendroseris* (Crawford et al. 1987), *Lactoris* (Crawford et al. 1994), *Rhaphithamnus* (A. Juss.) Moldenke (Crawford et al. 1993b), and *Wahlenbergia* Schrad. ex Roth (Crawford et al. 1990) are all consistent with those obtained from most other island groups. Only *Robinsonia* is anomalous in this pattern, having values comparable with continental flowering plant taxa (Crawford et al. 1992b), perhaps due to its dioecious sexual condition. By way of two examples, six species of *Dendroseris* were examined on Masatierra, and the results show very little genetic differentiation at gene loci encoding enzymes (Crawford et al. 1987). Some divergence does exist between the different subgenera, but very few differences occur between closely related species. The only known population of *Chenopodium sanctae-clarae* on Morro Spartan has also been examined. Its genetic variation is quite low, as might be expected, and indicates a fairly uniform gene pool (Crawford et al. 1988).

The consequence for conservation in taxa with low genetic variation is simply that very little adaptability is possible if environmental conditions change. However, it is important not to overreact to this problem, particularly in groups for which mainland relatives have not been analyzed carefully. For example, in *Chenopodium* it is noted that the genetic variation within *C. sanctae-clarae* is really no less than found among species in the continent (Wilson 1981). Hence, it is not known whether the species on Morro Spartan is any more depauperate genetically than any of the continental taxa and therefore, the seriousness of its low genetic variation must be balanced against a general tendency within the genus for low levels of variation. Moreover, there might be variation in other genetic systems not detected with present methods. Nonetheless, taxa such as those with few individuals and a restricted genetic base are much more susceptible to decimation by disease and other predators in changing environmental conditions. Therefore, it still should be a high priority to protect such fragile taxa by cultivation in botanical gardens. On the positive side, because of this genetic uniformity, there are no difficult decisions to be made on which part of the gene pool to attempt preservation through cultivation and/or cloning.

## RECOMMENDATIONS AND CONCLUSIONS

The Juan Fernandez Islands represent a small Pacific archipelago with a small endemic flora of which many species are endangered. As such it represents an opportunity to wage a strong effort to obtain positive results. This is particularly true for the nonshowy but evolutionarily most interesting paleoherb, the Lactoridaceae. The present impending threat to the family is posed by the noxious weed *Ugni molinae*.

Previous inventory work on the islands has clearly identified the endangered species. The strong efforts being made presently by CONAF of Chile are very positive and must be extended to a broader program with greater support. A plan of action seems feasible at this time. What is needed is a strong international program in cooperation with CONAF to provide the necessary resources for conservation to be effective. This should include control of exotic plants, eradication of recently introduced ornamentals (plus restrictions on reintroductions), removal of feral animals, and reforestation. The management plan of the Park (Anonymous 1976) provides many good ideas on conservation and reinforces points made here.

*Lantana camara* and *Lonicera japonica* are two very noxious weeds that still can be eradicated before they naturalize completely (Swenson et al. 1997). Restrictions on their reintroduction is necessary. Ecological studies and conservation strategies are urgently needed for other noxious weeds including *Acaena argentea*, *Aristotelia chilensis*, *Conium maculatum*, *Ipomoea indica*, *Rubus ulmifolius*, and *Ugni molinae* (Swenson et al. 1997). Obviously there is a great need to control *Rubus ulmifolius*. How this shall be accomplished is beyond the scope of this paper, but Smith (1990) emphasized that manual, ecological, chemical, or biological control strategies are used in management of Hawaii's National Parks. Whatever chemical or biological methods are used in the archipelago, ecological studies must be performed first in a restricted area before whole-scale application should be considered. The residual effects of any herbicide must be carefully calculated so that the overall ecosystem is not harmed.

Removal of feral animals is of paramount importance. Eradication of the numerous goats on Masafuera and rabbits on Masatierra must be given high priority. The pressure on the native flora brought about by these grazers is intense. They also are efficient dispersal agents for alien taxa such as *Acaena argentea*. It must be remembered, however, that goats also provide grazing pressure on the introduced weeds. Exclosure studies, therefore, are needed to understand how the native and alien floras respond ecologically to different management techniques and the subsequent removal of feral animals. Assuming a favorable response to such experiments, the number of goats should be lowered

by measures such (game) hunting, with perhaps some being left in a small fenced part of the island to serve as a source of meat for lobster fisherman.

The human population in San Juan Bautista should be encouraged to reduce their holdings of cattle, sheep, and horses, and to work with authorities on a plan that is adequate to their needs while at the same time not allowing animals to run wild throughout the native forest. Special corrals or feeding pens might be desirable in and around the village or in Valle Inglés, which has good pasture and no native vegetation on the lower slopes.

Reforestation of eroded areas should also be attempted, ideally by native species. The earlier, heavily eroded slopes of valley Colonial are now reforested with *Eucalyptus globulus* Labill. and *Pinus radiata* D. Don, and both are now naturalized and well established (Swenson et al. 1997). It would be preferable to reforest with native trees already adapted such as *Myrceugenia fernandeziana* Hook. et Arn. (Myrtaceae) and *Fagara mayu* (Bertero ex Savi) Engl. (Rutaceae). Planted in small groups and provided with necessary water, soil, and protection should enhance their ability to establish in badly eroded areas.

The Corporación Nacional Forestal (CONAF) has done an excellent job in developing a garden on Masatierra where some of the rare species are now being cultivated. Rare taxa of the archipelago must be restocked into the wild as well as being preserved in gardens on Masatierra, continental Chile, and elsewhere. Care must be taken that species do not hybridize indiscriminately in cultivation such that their integrity is lost. Further, there are several greenhouses in which seedlings have been started prior to establishment in the garden. Some of these have been returned to native surroundings, but success for permanent survival has been minimal. This has been especially true for the endemic palm, *Juania australis* (Mart.) Druce ex Hook.f. (Arecaceae; Stuessy et al. 1983). Village plantings in San Juan Bautista of rare taxa have also been encouraged and this has been successful as earlier mentioned regarding *Dendroseris litoralis* and *Che-nopodium sanctae-clarae*. Attempts must be made to save other taxa in this same fashion.

Most important in the overall conservation effort is to develop a suitable education program for the people of San Juan Bautista. As they have lived on the islands for many generations, they naturally view the land and the forests as their own, despite the fact that it is now a Chilean National Park. A useful educational project would be for the school children, supervised by their teachers, to help eradicate the abundant weed *Ipomoea indica*. This would be a good start toward developing ecological consciousness in the next generation as well as removing one of the potential threats to the native vegetation.



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## LITERATURE CITED

- ANONYMOUS. 1976. Plan de manejo Parque Nacional Juan Fernández. CONAF, Santiago, Chile.
- BARRIA, A. 1996. Incendio penetró bosque nativo en Juan Fernández. *El Mercurio*, February 22.
- BRAUNER, S. D., D. J. CRAWFORD, AND T. F. STUESSY. 1992. Ribosomal DNA and RAPD variation in the rare plant family Lactoridaceae. *Amer. J. Bot.* **79**: 1436–1439.
- BREMER, K. 1994. Asteraceae: cladistics and classification. Timber Press, Portland, Oregon.
- CARLQUIST, S. 1965. Island life: a natural history of the islands of the world. Natural History Press, New York. 455 p.
- . 1974. Island Biology. Columbia University Press, New York. 660 p.
- . 1990. Wood anatomy and relationships of Lactoridaceae. *Amer. J. Bot.* **77**: 1498–1505.
- CRAWFORD, D. J., S. BRAUNER, M. B. COSNER, AND T. F. STUESSY. 1993a. Use of RAPD markers to document the origin of the intergeneric hybrid *×Margaracaena skottsbergii* (Rosaceae) on the Juan Fernandez Islands. *Amer. J. Bot.* **80**: 89–92.
- , T. F. STUESSY, M. B. COSNER, D. W. HAINES, M. SILVA O., AND M. BAEZA. 1992a. Evolution of the genus *Dendroseris* (Asteraceae, Lactuceae) on the Juan Fernandez Islands: evidence from chloroplast and ribosomal DNA. *Syst. Bot.* **17**: 676–682.
- , ———, ———, ———, D. WIENS, AND P. PEÑAILILLO. 1994. *Lactoris fernandeziana* (Lactoridaceae) on the Juan Fernandez Islands: allozyme uniformity and field observations. *Conservation Biol.* **8**: 277–280.
- , ———, D. W. HAINES, M. B. COSNER, M. SILVA O., AND P. LOPEZ. 1992b. Allozyme diversity within and divergence among four species of *Robinsonia* (Asteraceae: Senecioneae), a genus endemic to the Juan Fernandez Islands, Chile. *Amer. J. Bot.* **79**: 962–966.
- , ———, T. G. LAMMERS, M. SILVA O., AND P. PACHECO. 1990. Allozyme variation and evolutionary relationships among three species of *Wahlenbergia* (Campanulaceae) in the Juan Fernandez Islands. *Bot. Gaz. (Crawfordsville)* **151**: 119–124.
- , ———, R. RODRIGUEZ, AND M. RONDINELLI. 1993b. Genetic diversity in *Rhaphithamnus venustus* (Verbenaceae), a species endemic to the Juan Fernandez Islands. *Bull. Torrey Bot. Club* **120**: 23–28.
- , ———, AND M. SILVA O. 1986. Leaf flavonoid chemistry and the relationships of the Lactoridaceae. *Pl. Syst. Evol.* **153**: 133–139.
- , ———, AND ———. 1987. Allozyme divergence and the evolution of *Dendroseris* (Compositae: Lactuceae) in the Juan Fernandez Islands. *Syst. Bot.* **12**: 435–443.
- , ———, AND ———. 1988. Allozyme variation in *Chenopodium sanctae-clarae*, an endemic species of the Juan Fernandez Islands, Chile. *Biochem. Syst. & Ecol.* **16**: 279–284.
- CRUZ, F., J. CRUZ, AND J. LAWESSON. 1986. *Lantana camara* L., a threat to native plants and animals. *Not. Galapagos* **43**: 10–11.
- DOYLE, J. A. 1994. Origin of the angiosperm flower: a phylogenetic perspective, pp. 7–30. In P. K. Endress and E. M. Friis [eds.], *Early evolution of flowers*. Springer-Verlag, Wien.
- GAY, C. 1854. Atlas de la historia física y política de Chile. Paris, France.
- GONZALEZ-FERRAN, O. 1987. Geological evolution of Chilean Pacific Oceanic islands, pp. 39–54. In J. C. Castilla [ed.], *Islas Oceánicas Chilenas: conocimiento científico y necesidades de investigaciones*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- HARRIS, L. D. 1984. The fragmented forest. The University of Chicago Press, Chicago.
- HELENURM, K., AND F. R. GANDERS. 1985. Adaptive radiation and genetic differentiation in Hawaiian *Bidens*. *Evolution* **39**: 753–765.
- HERNANDEZ, R., AND J. MONLEON. 1975. La comunidad de pescadores de Juan Fernández, pp. 137–153. In M. Orellana [ed.], *Las Islas de Juan Fernández. Departamento ciencias antropológicas y arqueológicas*, Santiago, Chile.
- HOFFMANN, A. J., AND C. MARTICORENA. 1987. La vegetación de las Islas Oceánicas Chilenas, pp. 129–165. In J. C. Castilla [ed.], *Islas Oceánicas Chilenas: conocimiento científico y necesidades de investigaciones*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- JOHNS, F. 1896. Estudios sobre la flora de las Islas de Juan Fernández. Chilean Government, Santiago, Chile.
- LAMMERS, T. G., T. F. STUESSY, AND M. SILVA O. 1986. Systematic relationships of the Lactoridaceae, an endemic family of the Juan Fernandez Islands, Chile. *Pl. Syst. Evol.* **152**: 243–266.
- LAWESSON, J. E., AND L. ORTIZ. 1990. Plantas introducidas en las Islas Galapagos. *Monogr. Syst. Bot. Missouri Bot. Gard.* **32**: 201–210.
- LOOSER, G. 1927. La zarzamora (*Rubus ulmifolius* Schott) en Juan Fernandez. *Revista Chilena Hist. Nat.* **31**: 85–86.
- LOWREY, T. K., AND D. J. CRAWFORD. 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Astereae) on the Hawaiian Islands. *Syst. Bot.* **10**: 64–72.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- MATTHEI, O. 1995. Manual de las Malezas que crecen en Chile. Published by the Author, Santiago, Chile.
- , C. MARTICORENA, AND T. F. STUESSY. 1993. La flora adventicia del archipiélago de Juan Fernández. *Bol. Soc. Biol. Concepción Chile* **57**: 69–102.
- OEHRNS, E., AND N. GARRIDO. 1986. Posibilidad del control biológico de la zarzamora en el archipiélago de Juan Fernández. *Bol. Soc. Biol. Concepción Chile* **57**: 205–206.
- PACHECO, P., T. F. STUESSY, AND D. J. CRAWFORD. 1991. Natural interspecific hybridization in *Gunnera* (Gunneraceae) of the Juan Fernandez Islands, Chile. *Pacific Sci.* **45**: 389–399.
- QIU, Y.-L., M. W. CHASE, D. H. LES, AND C. R. PARKS. 1993. Molecular phylogenies of the Magnoliidae: cladistic analyses of nucleotide sequences of the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* **80**: 587–606.
- RICCI, M. 1995. [No title given]. *Noticero Jardin Botánico Nacional* **3**: 1. CONAF, Chile.
- RINGROSE, B. 1685. *Bucaniers of America*, Ed. 2. London, England.
- SANDERS, R. W., T. F. STUESSY, AND C. MARTICORENA. 1982. Recent changes in the flora of the Juan Fernandez Islands, Chile. *Taxon* **31**: 284–289.

- , ———, ———, AND M. SILVA O. 1987. Phytogeography and evolution of *Dendroseris* and *Robinsonia*, tree-like Compositae of the Juan Fernandez Islands. *Opera Bot.* **92**: 195–215.
- , ———, AND R. RODRIGUEZ. 1983. Chromosome numbers from the flora of the Juan Fernandez Islands. *Amer. J. Bot.* **70**: 799–810.
- SANG, T., D. J. CRAWFORD, S.-C. KIM, AND T. F. STUESSY. 1994. Radiation of the endemic genus *Dendroseris* (Asteraceae) on the Juan Fernandez Islands: evidence from sequences of the ITS regions of nuclear ribosomal DNA. *Amer. J. Bot.* **81**: 1494–1501.
- SCHWAAR, J. 1979. Feuchtwalder auf Juan Fernandez. *Phytocoenologia* **6**: 514–523.
- SIMBERLOFF, D., AND L. G. ABELE. 1982. Refuge design and island biogeographic theory: effects of fragmentation. *Amer. Nat.* **120**: 41–50.
- SKOTTSBERG, C. 1910. Juan Fernandez-öarnas sandelträd. *Svensk Bot. Tidskr.* **4**: 167–173.
- . 1921. The phanerogams of the Juan Fernandez Islands. *Natural History of Juan Fernandez and Easter Island*. **2**: 95–240.
- . 1951. A supplement to the pteridophytes and phanerogams of Juan Fernandez and Easter Island. *Natural History of Juan Fernandez and Easter Island*. **2**: 763–792.
- . 1953. The vegetation of the Juan Fernandez Islands. *Natural History of Juan Fernandez and Easter Island*. **2**: 793–960.
- . 1956. Derivation of the flora and fauna of Juan Fernandez and Easter Island; part 1, The Juan Fernandez Islands. *Natural History of Juan Fernandez and Easter Island*. **1**: 194–405.
- SMITH, C. W. 1990. Weed management in Hawaii's National Parks. *Monogr. Syst. Bot. Missouri Bot. Garden* **32**: 223–234.
- SPOONER, D. M., T. F. STUESSY, D. J. CRAWFORD, AND M. SILVA O. 1987. Chromosome numbers from the flora of the Juan Fernandez Islands. II. *Rhodora* **89**: 351–356.
- STUESSY, T. F. 1995. Juan Fernandez Islands—Chile, pp. 565–568. In S. D. Davis, V. H. Heywood, and A. C. Hamilton [eds.], *Centres of plant diversity: a guide and strategy for their conservation*, Vol. 3. World Wildlife Fund, International Union for the Conservation of Nature, Cambridge, United Kingdom.
- , D. J. CRAWFORD, AND C. MARTICORENA. 1990. Patterns of phylogeny in the endemic vascular flora of the Juan Fernandez Islands, Chile. *Syst. Bot.* **15**: 338–346.
- , K. A. FOLAND, J. F. SUTTER, R. W. SANDERS, AND M. SILVA O. 1984a. Botanical and geological significance of potassium-argon dates from the Juan Fernandez Islands. *Science* **225**: 49–51.
- , C. MARTICORENA, R. RODRIGUEZ, D. J. CRAWFORD, AND M. SILVA O. 1992. Endemism in the vascular flora of the Juan Fernandez Islands. *Aliso* **13**: 297–307.
- , R. W. SANDERS, AND O. R. MATTHEI. 1983. *Juania australis* revisited in the Juan Fernandez Islands, Chile. *Principes* **27**: 71–74.
- , ———, AND M. SILVA O. 1984b. Phytogeography and evolution of the flora of the Juan Fernandez Islands: a progress report, pp. 55–69. In Radovsky, P. H. Raven, and S. H. Sohmer [eds.], *Biogeography of the tropical Pacific*. Association of Systematic Collections and The Bishop Museum, Lawrence, Kansas.
- SUN, B. Y., T. F. STUESSY, AND D. J. CRAWFORD. 1990. Chromosome counts from the flora of the Juan Fernandez Islands, Chile. III. *Pacific Sci.* **44**: 258–264.
- , A. M. HUMAÑA, M. RIVEROS G., AND D. J. CRAWFORD. 1996. Evolution of *Rhaphithamnus venustus* (Verbenaceae), a gynodioecious hummingbird-pollinated endemic of the Juan Fernandez Islands, Chile. *Pacific Sci.* **50**: 55–65.
- SWENSON, U., T. F. STUESSY, M. BAEZA, AND D. J. CRAWFORD. 1997. New and historical plant introductions, and potential pests in the Juan Fernandez Islands, Chile. *Pacific Sci.* **51**: 233–253.
- TOBE, H., T. F. STUESSY, P. H. RAVEN, AND K. OGNUMA. 1993. Embryology and karyomorphology of Lactoridaceae. *Amer. J. Bot.* **80**: 933–946.
- VALDEBENITO, H., T. F. STUESSY, AND D. J. CRAWFORD. 1990. A new biogeographic connection between islands in the Atlantic and Pacific Ocean. *Nature* **347**: 549–550.
- WAGNER, W. L., D. R. HERBST, AND S. H. SOHMER. 1990. *Manual of the flowering plants of Hawaii*, Vol. 1 and 2. Bishop Museum, Honolulu.
- WESTER, L. 1991. Invasions and extinctions on Masatierra (Juan Fernandez Islands): a review of early historical evidence. *J. Hist. Geogr.* **17**: 18–34.
- WILSON, H. D. 1981. Genetic variation among South American populations of tetraploid *Chenopodium* sect. *Chenopodium* subsect. *Cellulata*. *Syst. Bot.* **6**: 380–398.
- WITTER, M. S., AND G. D. CARR. 1988. Adaptive radiation and genetic differentiation in the Hawaiian silversword alliance (Compositae-Madiinae). *Evolution* **42**: 1278–1287.
- WOODWARD, R. L. 1969. *Robinson Crusoe's Island: a history of the Juan Fernandez Islands*. The University of North Carolina Press, Chapel Hill.
- ZAVADA, M. S., AND J. M. BENSON. 1987. First fossil evidence for the primitive angiosperm family Lactoridaceae. *Amer. J. Bot.* **74**: 1590–1594.