Aliso: A Journal of Systematic and Evolutionary Botany

Volume 13 | Issue 2 Article 3

1992

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ALISO
13(2), 1992, pp. 297–307

ENDEMISM IN THE VASCULAR FLORA OF THE JUAN FERNANDEZ ISLANDS

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ABSTRACT

The Juan Fernandez archipelago contains 361 vascular plant species including 53 ferns, 65 monocots, and 243 dicots. Represented are 73 families and 219 genera. There is one endemic family (Lactoridaceae), 12 endemic genera, and 126 endemic species. The native vascular flora has 11% endemism at the generic level and 60% at the specific level. Among the endemic species, 23 are ferns, 15 are monocots, and 88 are dicots. Of the endemic dicots, 29 species are Compositae, making up 33% of the endemic dicot flora. Most (97%) of the endemic angiosperms are perennials, and 64% of the dicots are woody (shrubs, rosette-trees, and trees). The endemic angiosperms are found in all of the major ecological zones in the islands: fern forest; dry forest; alpine zone; open ridges and cliffs; dry, open slopes; canyons (quebradas); and the shore. They are most abundant in the dry forest (38%) and open ridges and cliffs (22%). There is no evidence of change in chromosome number during evolution of the endemic dicots, and genetic differences between congeneric endemic species at isozyme loci are minimal. The endemic angiosperms are definitely in a fragile state with 75% of the species being regarded as either extinct, threatened, rare, or occasional. *Santalum fernandezianum* (Santalaceae) is definitely extinct, and *Dendroseris macrantha* (Compositae) presumed so.

Key words: endemism, island evolution, Juan Fernandez Islands.

INTRODUCTION

The Juan Fernandez Islands lie 600 km W of continental Chile at 33° south latitude. This archipelago consists of three principal islands: Masatierra, Santa Clara (just offshore from Masatierra), and Masafuera. Radiometric datings have been obtained from these islands and Masatierra (including Santa Clara) is approximately 4 million years old, and Masafuera, which lies 150 km further west from Masatierra, is 1 to 2 million years old (Stuessy et al. 1984*a*). These islands harbor a subtropical flora with a high degree of endemism.

The most significant studies on the endemic flora of the Juan Fernandez Islands have been those of Skottsberg (1922, 1951, 1953, 1956). In these important publications, which were summarized in the three-volume *Natural History of the Juan Fernandez and Easter Islands,* he provided the basic inventory of the flora of the islands which provided a foundation for detailed evolutionary studies. Our collaborative work between laboratories at the Ohio State University and the Universidad de Concepción has examined the endemic species of the archipelago from the standpoint of evolutionary patterns and processes.

To understand plant evolution in any island archipelago requires focusing primarily on the endemic flora. These elements offer more information about biogeographic events which can then be used to suggest patterns of phylogeny and modes of speciation. Studies of the introduced flora are also important, particularly as they impact the conservation status of the native and endemic members, but

Table 1. Number of vascular plant taxa present in the Juan Fernandez Islands.

	Families	Genera	Species
Ferns	12	26	53
Dicots	56	148	243
Monocots	7	39	65
Totals	75	213	361

they are primarily of historical interest in the development of the weedy flora and human activities rather than for understanding modes of organic evolution.

The purposes of this paper are to: 1) give a statistical summary of the entire vascular flora; 2) present additional statistics for only the endemic taxa; 3) comment on biological aspects of the endemic angiosperms including habit, reproductive strategies, ecological zonation, and chromosomal variation; 4) discuss genetic variation, phylogeny and modes of speciation within the endemic taxa; and 5) comment on their conservation status.

STATISTICS OF THE VASCULAR FLORA

The numbers of taxa that are known to be extant in the Juan Fernandez Islands are shown in Table 1. There are 361 vascular plant species, of which 53 (15%) are ferns, 65 (18%) are monocots, and 243 (67%) are dicots. A total of 75 families and 213 genera are represented.

The number of taxa in the islands can be analyzed further into introduced, native, and endemic categories (Tables 2 and 3). There is only one endemic family, Lactoridaceae, whereas there are 28 native families as well as 46 introduced ones. Large numbers of introduced taxa, particularly dicots, have accumulated within historical time since 1574 when the Islands were discovered (Woodward 1969). There are 213 total genera; approximately half (107) of these are introduced. There are 12 endemic genera, including 7 dicot genera. The species reveal a similar pattern (Table 3) with 42% introduced and 58% endemic and native. The largest group of introduced taxa is the dicots (82%). Within the endemic and native categories, there are 209 species, of which 83 can be regarded as native, and the remaining 126 as endemic. Most important for our discussion are these endemic species, and particularly the 103 angiosperms.

STATISTICS OF THE ENDEMIC TAXA

The numbers of endemic families, genera, and species of the Juan Fernandez flora are shown in Table 4. Sixty percent of the toal vascular flora is endemic, and 65% for the angiosperms. At the generic level there is 11% endemism of the total vascular flora and 14% for the angiosperms. These figures differ slightly from those given earlier by Skottsberg (1956; 68.7% endemism for species and 19% for genera), but the trends are the same.

The archipelago has a large number of endemic genera. Among the ferns is *Thyrsopteris* (Dicksoniaceae, 1 species). Of the dicots there are: *Centaurodendron* (Compositae, 2 spp.); *Cuminia* (Labiatae, 2 spp.); *Dendroseris* (Compositae, 11 spp.); *Lactoris* (Lactoridaceae, 1 sp.); *Robinsonia* (Compositae, 7 spp.); *Selkirkia* (Boraginaceae, 1 sp.); and *Yunquea* (Compositae, 1 sp.). Among monocots the

Table 2. Number of endemic, native and introduced families/genera of vascular plants in the Juan Fernandez Islands.

	Endemic	Native	Introduced	Total
Ferns	0/1	12/25	0/0	12/26
Dicots	1/7	12/50	43/91	56/148
Monocots	0/4	4/19	3/16	7/39
Totals	1/12	28/94	46/107	75/213

endemic genera are: *Juania* (Palmae, 1 sp.); *Megalachnae* (Gramineae, 2 spp.); *Ochagavia* (Bromeliaceae, 1 sp.); and *Podophorus* (Gramineae, 1 sp.). There are 31 species in these endemic genera, representing 25% of the endemic species in the Islands. This suggests that any study of patterns and processes of evolution in the archipelago should take into account these endemic genera.

Table 5 indicates the number of species in different families of ferns and their distribution in the archipelago. The Hymenophyllaceae have the highest number of endemic species, and this might be expected from the high levels of taxa on the adjacent Chilean continent in the moist Magellanic forest (Gunckel 1984). The Dryopteridaceae and Blechnaceae are also well represented with four endemic species each. Perhaps more interesting is the distribution on the major islands of the 23 endemic species of ferns; most (16) seem to have no difficulty dispersing and establishing in both islands, with only three restricted to Masafuera and five to Masatierra.

For the monocots, however, the situation is somewhat different (Table 6). Only six families are represented with the grasses being most abundant. The distributional patterns show a reasonably even distribution of endemic taxa on one or the other of the islands, with only four species found on both.

Table 7 indicates endemic species of dicots in 31 different families. In particular, the Compositae contain 29 endemic species, representing 33% of the total species in these families. This makes members of the Compositae especially good candidates for evolutionary study. This is perhaps not surprising, for the family is also well represented in other isolated archipelagoes such as Hawaii (Wagner, Herbst, and Sohmer 1990). Once again, the endemic species in Juan Fernandez tend to be distributed on one or the other of the major islands rather than on both. Only 11 of the 90 species are found on both of the major islands. Forty-seven species are exclusively found on Masatierra and 30 on Masafuera. Except for the Compositae, there are many families with a small number of species making up the endemic dicot flora.

Table 3. Number of endemic, native, and introduced species (% of total across table/% down table) of vascular plants in the Juan Fernandez Islands.

	Endemic	Native	Introduced	Total
Ferns	23 (45%/18%)	28 (55%/34%)	0 (0%/0%)	53 (15%)
Dicots	88 (36%/10%)	30 (12%/36%)	125 (51%/82%)	243 (67%)
Monocots	15 (23%/12%)	25 (39%/30%)	27 (42%/18%)	65 (18%)
Totals	126 (35%)	83 (23%)	152 (42%)	361

Table 4. Number of endemic taxa (and % of native and endemic vascular flora) in the Juan Fernandez Islands.

	Families	Genera	Species
Ferns	0 (0%)	1 (3%)	23 (45%)
Dicots	1 (8%)	7 (12%)	88 (75%)
Monocots	0 (0%)	4 (17%)	15 (38%)
Totals	1	12	126

BIOLOGICAL ASPECTS OF THE ENDEMIC ANGIOSPERMS

It is of interest to examine correlations of the endemic angiosperms with selected biological features. Of particular relevance is the high degree of woodiness in the flora which is typical of island plants (Carlquist 1974). Sixty-four percent of the dicots are either trees (16%), rosette-trees (28%), or shrubs (20%). The monocots, obviously, have few woody representatives except for *Juania australis* (Mart.) Drude ex Hook. f. The high representation of the woody habit may reflect to some degree the filling of ecological niches in the islands by groups not ordinarily disposed to the woody condition in continental source areas, such as evidenced by the woody *Plantago fernandezia* Bertero ex Barneoud (Plantaginaceae). Most of the monocots are perennial herbs, and this is true also for a large percentage of the dicots (33%).

The endemic taxa are distributed into ecological zones as shown in Table 8. All of these zones are found on Masafuera; on Masatierra the alpine zone is lacking. Also, the quebrada (canyon) zone consists of very deep ravines to 500 meters on Masafuera, whereas on Masatierra they are much broader and shallower as a result of more erosion. Most of the species of the flora are found in the dry forest (38%) and open ridges and cliffs (20%). Fewer species occur in the alpine zone (13%) and shore (12%). Still fewer species are confined to the dry open slopes (9%); quebradas (5%), or the fern forests (4%). The dry open slopes are now heavily covered by introduced grasses such as *Anthoxanthum odoratum* L. The quebradas and fern forests are simply smaller in area and have fewer taxa overall. The shore

Table 5. Families of ferns in the Juan Fernandez Islands giving numbers of endemic species and distributions in the archipelago.

Family	Number of endemic species	Distribution		
		MF	MT	MT and MF
Adiantaceae	2			2
Aspleniaceae	2			2
Blechnaceae	4	1		3
Dicksoniaceae	3	1	1	1
Dryopteridaceae	4			4
Gleicheniaceae	1	1		
Hymenophyllaceae	5		3	2
Ophioglossaceae	1		1	
Polypodiaceae	1	—	—	1
Totals	23	3	5	15

Table 6. Families of monocots in the Juan Fernandez Islands with numbers of endemic species and distributions in the archipelago.

Family	Number of species	Distribution MF	MT	MT and MF
Bromeliaceae	2		2	
Cyperaceae	4	1	1	2
Gramineae	6	2	2	2
Juncaceae	1	1		
Orchidaceae	1	1		
Palmae	1		1	
Totals	15	5	6	4

Table 7. Families of dicots in the Juan Fernandez Islands with numbers of endemic species and distributions in the archipelago.

Family	Number of endemic Species	Distribution MF	MT	MT and MF
Berberidaceae	2	1	1	
Boraginaceae	1		1	
Campanulaceae	3	1	2	
Caryophyllaceae	2	1		1
Chenopodiaceae	3	1	2	
Compositae	29	10	17	2
Cruciferae	1	1		
Ericaceae	1			1
Euphorbiaceae	1		1	
Flacourtiaceae	1		1	
Gunneraceae	3	1	2	
Haloragaceae	2	1	1	
Labiatae	2		2	
Lactoridaceae	1		1	
Leguminosae	2	1	1	
Myrtaceae	3	1	2	
Piperaceae	3	1	1	1
Plantaginaceae	1		1	
Ranunculaceae	1	1		
Rhamnaceae	1		1	
Rosaceae	3	1	2	
Rubiaceae	3	1	1	1
Rutaceae	2	1	1	
Santalaceae	1			1
Saxifragaceae	1		1	
Scrophulariaceae	2	2		
Solanaceae	3	2	1	
Umbelliferae	4	1	3	
Urticaceae	4	1	1	2
Verbenaceae	1			1
Winteraceae	1			1
Totals	88	30	47	11

Table 8. Occurrence of endemic angiosperms in ecological zones in the Juan Fernandez Islands.

Ecological zone	Number of species		
	Dicots	Monocots	Monocots and dicots
Fern forest	3 (3%)	1 (7%)	4 (4%)
Dry forest	32 (36%)	7 (47%)	39 (38%)
Alpine zone	11 (13%)	2 (13%)	13 (13%)
Open ridges and cliffs	19 (22%)	2 (13%)	21 (20%)
Dry, open slopes	8 (9%)	1 (7%)	9 (9%)
Quebradas	4 (5%)	1 (7%)	5 (5%)
Shore	11 (13%)	1 (7%)	12 (12%)
Total	88	15	103

area does reveal a reasonably high level of endemism, and the endemic taxa compete for survival in this zone with the introduced weeds which are constantly arriving there.

Although few studies have dealt directly with reproductive systems in the endemic flora of Juan Fernandez, it appears that all of the monocots are hermaphroditic, whereas this is true for only 86% of the dicots. *Cuminia* (Labiatae) is apparently monoecious, although this needs to be confirmed experimentally. This gives a 2% level of monoecy for the endemic flora. Three genera are dioecious: *Robinsonia* (Compositae, 7 spp.); *Coprosma* (Rubiaceae, 2 spp.); and *Fagara* (Rutaceae, 2 spp.). The high level of dioecy (12% of the endemic flora) corresponds with high levels also documented in other oceanic archipelagos (e.g., Carlquist 1974). The reasons for this are unclear, although it has been suggested that there is selection for outcrossing to promote genetic heterozygosity (Carlquist 1974). However, it also has been suggested that the taxa that normally arrive in oceanic islands may come from comparable climatic zones in continental source areas also with higher levels of dioecy (Baker and Cox 1984).

Chromosomal surveys have been made from the endemic species of Juan Fernandez to determine the importance of chromosomal changes during evolution in the archipelago, and to assess changes in chromosome number from progenitors in source areas. Thirty-eight species have now been counted from 69 populations, including reports from Sanders, Stuessy, and Rodriguez (1983), Spooner, Stuessy, Crawford, and Silva (1984), and Sun, Stuessy, and Crawford (1990). Forty-three percent of the endemic dicots have been counted, but none of the endemic monocots has been examined so far. As a result of these data, one can offer some observations and suggestions. Thirty-one percent of the endemic species show neither ancient nor recent polyploidy. That is, they show no obvious polyploidy from continental relatives nor are the relatives at a presumed polyploidy level. Approximately two thirds of the flora, however, are probably precolonizaton polyploids, i.e., they and their ancestors are at chromosomal levels of $n = 12$ or higher. Only 6% are perhaps recent polyploids, and these are *Ugni selkirkii* (H. et A.) Berg (Myrtaceae) and *Spergularia confertiflora* Steud. (Caryophyllaceae). Six percent are possibly of aneuploid origin, and these would be the three counted species of *Wahlenbergia* (Campanulaceae) at $n = 11$, whereas the apparent generic relatives are $n = 9$ (Sanders et al. 1983). Seventy-four percent of the species counted are also woody, but this closely parallels the percentage of woodiness (64%) of the entire endemic dicot flora.

An important point about the cytology of the endemic flora is that no reticulate evolution (i.e., hybridization or polyploidy) has occurred in the evolution of endemic taxa in the archipelago. Chromosomal change from progenitors to derivatives in the islands appears also to have been minimal. Furthermore, there is no evidence of intra- or interisland chromosomal change within particular lineages. These results coincide with those that have been obtained recently from the Bonin islands by M. Ono (1991), as well as those documented by Carr (1978, 1985) for the Hawaiian flora. Apparently evolution is extremely rapid within oceanic archipelagos, but this is not usually accompanied by change in chromosome number.

GENETIC VARIATION, PHYLOGENY, AND MODES OF SPECIATION IN THE ENDEMIC FLORA

Our investigations on the evolution of the vascular flora of the Juan Fernandez Islands have focused on the genera that have three or more endemic species. Two endemic species can give some information on patterns of phylogeny and modes of speciation, but three can be even more informative. Genera with three or more endemic species in the archipelago are as follows: ferns: *Blechnum* (4 spp.), *Asplenium* (3); dicots: *Dendroseris* (11), *Robinsonia* (7), *Erigeron* (6), *Wahlenbergia* (3), *Eryngium* (4), *Solanum* (4), *Chenopodium* (3), *Gunnera* (3), and *Peperomia* (3). Twenty-four of these endemic species are found in *Dendroseris, Robinsonia,* and *Erigeron.* This makes the Compositae a particularly good focus for any evolutionary investigation, and for this reason we have already placed particular emphasis on this family (e.g., Crawford, Stuessy, and Silva 1987; Sanders, Stuessy, Marticorena, and Silva 1987).

Studies on genetic variation have been completed on *Dendroseris, Wahlenbergia,* and *Chenopodium.* In *Dendroseris,* six of the species representing two of the subgenera have been analyzed (Crawford et al. 1987). Little divergence among species was found within each of the subgenera, but some difference was found between subgenera. The results indicate that very low levels of measurable genetic divergence exist among these species, despite the fact that they are extremely different morphologically. In fact, the subgenera in the past have been recognized by some workers as distinct genera (e.g., Skottsberg 1951). This same situation has also been documented among the more recently evolved silverswords of the family from Hawaii (Witter and Carr 1988). Studies on *Wahlenbergia* of the Campanulaceae have just been finished (Crawford, Stuessy, Lammers, and Silva 1990), and the results differ from *Dendroseris.* One species, *W. fernandeziana* A. DC., is quite variable at isozyme loci, with two or more alleles detected at several loci. The two other species [*W. berteroi* H. et A. and *W. masafuerae* (Phil.) Skottsb.], by contrast, contain the same subset of the variation detected in *W. fernandeziana.* This suggests that *W. fernandeziana* may have given rise to *W. berteroi* and *W. masafuerae* via founder events. In *Chenopodium* (Chenopodiaceae), the endemic species *C. sanctae-clarae* Johow is confined to a single rock, Morro Spartan, just off the coast of Santa Clara. There are approximately 20 individuals inhabiting this rock, and these show a very low level of genetic diversity (Crawford, Stuessy, and Silva 1988). Such low levels might be expected within an extremely rare taxon, but the levels of allozymic variation in continental species of the same genus are also extremely low (Wilson 1981). The suggestion

Table 9. The conservation status of endemic angiosperm species in the Juan Fernandez Islands.

Status	Number of species		
	Monocots	Dicots	Monocots and dicots
Extinct		2 (2%)	2 (2%)
Threatened	2 (13%)	15 (17%)	17 (17%)
Rare	5 (33%)	29 (33%)	34 (33%)
Occasional	3 (20%)	21 (24%)	24 (23%)
Common	5 (33%)	13 (15%)	18 (18%)
Abundant		8 (9%)	8 (8%)
Totals	15	88	103

that the low diversity is a result solely of founder events in this case, therefore, cannot be substantiated.

Analysis of phylogenetic patterns within the Juan Fernandez archipelago has revealed several interesting points. There are only 15 different patterns of distribution among the endemic species of all the vascular flora (Stuessy, Crawford, and Marticorena 1990). More importantly, these distributional patterns can be analyzed in the context of general patterns of phylogeny (i.e., cladogenesis, anacladogenesis, and anagenesis). Although these terms are relative, anagenetic evolutionary change (i.e., change within a lineage) has been most common in the archipelago. Many species apparently have dispersed to another island or have come from the continent to the original island and speciated through time within that same lineage without splitting events taking place. As a result, this provides an opportunity to study degrees of genetic change during speciation in distinct lines within a known time frame. Studies of molecular phylogeny in the context of ecological change, which we are now beginning to pursue, will be particularly appropriate here.

The distributional patterns and the low levels of allozymic divergence among the endemic species clearly suggest very rapid evolution. Studies completed on *Erigeron* (Compositae) on Masafuera, the younger island, suggest that species did partition ecologically during speciation (Valdebenito 1989). On Masatierra it is more difficult to assess the impact of adaptive radiation, because the flora has apparently been compacted and the ecological zones are not as clear as they once were. The size of the island might have been reduced in area as much as 80% during the past 4 million years (Stuessy, Sanders, and Silva 1984*b*). The pattern of speciation appears to be one of rapid morphological change based on few genetic differences accompanied by geographical isolation and ecological differentiation. Supporting such a possibility are the deep ravines (quebradas) which sometimes plunge 500 meters (as now seen on Masafuera). Relief of this nature provides many microhabitats and would serve as a strong stimulus for ecological zonation.

CONSERVATION STATUS OF THE ENDEMIC ANGIOSPERMS

The conservation status of the endemic angiosperm species of Juan Fernandez is shown in Table 9. We have used these categories: extinct, threatened, rare, occasional, common, and abundant. "Extinct" is self explanatory. "Threatened"

Table 10. Relationship of conservation status to habit of the endemic angiosperms in the Juan Fernandez Islands.

Habit	Conservation status: Extinct	Threatened	Rare
Tree	1		2
Rosette-tree	1	7	12
Shrub		5	3
Perennial herb		3	17
Annual		1	2

means that only a single population is left, as far as we know. "Rare" means that several populations are known with at least a few individuals in each. "Occasional" refers to having scattered populations throughout the islands, and "common" means that there are significant numbers of populations and individuals per population. "Abundant" indicates that a species is found extensively on the island throughout its ecological zone. The overall picture for the 103 endemic species is one of considerable rarity (Table 9). Two species of dicots are extinct. One is *Santalum fernandezianum* Phil., which disappeared toward the beginning of this century (Skottsberg 1956). The other extinct taxon is apparently *Dendroseris macrantha* (Bertero ex Decne.) Skottsb., which we found growing in a private garden in the village of San Juan Bautista in December of 1980. It has now been cut down and no other individuals have been found by us. Seventeen percent of the endemic angiosperms are threatened, 33% are rare, and 23% are occasional. The threatened and rare categories comprise 50% of the angiosperm flora and 73% for the combined threatened, rare, and occasional classes. Most of the flora, therefore, is in a delicate condition with regard to its survival for the future. Only 18% of the species can be regarded as common and only 8% as abundant.

The extinct, threatened, and rare categories can be related to the habit of the plants (Table 10). Basically all of the categories are under pressure for one reason or another, with the trees and rosette-trees having been cut for firewood, ship repair, and other construction uses. The shrubs, perennial herbs, and annuals have come under tremendous pressure from feral and domestic animals, especially goats, which presently number some 5000–10,000 on Masafuera (Sanders, Stuessy, and Marticorena 1982). All categories, therefore, have come under pressure from human influence.

In looking at the common and abundant species to see if any particular survival strategies emerge, there is no syndrome that is pervasive. Four monocots [*Carex berteroana* Steud., *Chaetotropis imberbis* (Phil.) Björkman, *Megalachne berteroana* Steud., and *Uncinia douglassii* Boott] and four dicots [*Erigeron fernandezianus* (Colla) Solbrig, *Pernettya rigida* (Bertero ex Colla) DC., *Rhaphithamnus venustus* (Phil.) B. L. Robins., and *Spergularia confertiflora*) have been quite successful, and most of these are perennial herbs. Two shrubs and one tree (*Rhaphithamnus*) also are common. These successful species are found in different ecological zones and at different elevations, which suggests that it is not a matter of a particular zone serving as a refuguim, but rather the ability of individual species to be aggressive and compete effectively with the introduced weeds.

CONCLUSION

The Juan Fernandez Islands contain a delicate balance of monocots, dicots, and ferns which, from a conservation perspective, need immediate attention for future survival. An important step would be the elimination of the feral animals which plague both islands, but most particularly on Masafuera. Human activity has been more dramatic on Masatierra, where there has been a permanent settlement for most of the past two centuries (Woodward 1969), and where more weeds have been introduced and more active destruction of the forest has occurred. In previous centuries Masatierra served as a base for refitting and reconditioning of ships after they rounded Cape Horn and before continuing westward into the Pacific to complete around-the-world voyages (Woodward 1969).

Because of the small size of the archipelago, the limited number of endemic species, and the close relationship to the major source areas in continental South America, the Juan Fernandez Islands provide an excellent natural laboratory for studying plant speciation. The basic conclusions so far are that speciation has occurred very rapidly via adaptive radiation and ecological zonation with no chromosomal change and with very little genetic alteration, but with maximum morphological divergence. In fact, in oceanic archipelagos, such as the Juan Fernandez Islands, a situation exists in which minimal genetic change occurs during speciation. Because there is also maximum morphological alteration, these are perhaps the best systems in the world in which to examine the effects of genetic change on speciation and also the relationship of morphological adaptation to ecological factors during evolution.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the National Science Foundation for support under grants INT77-21637 and BSR83-06436 to TFS and DJC; CONICYT for support to MS; the University of Concepción for support to MS, CM, and RR; CONAF of Chile for permission to collect in the Islands; and Bernardo Ackermann, Gastón Gonzaléz, and Ivan Laeva, recent Chiefs of the Juan Fernandez National Park, for their help in facilitating our research while in the Islands.

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