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ALLOZYME DIVERSITY IN ENDEMIC FLOWERING PLANT SPECIES OF THE JUAN FERNANDEZ ARCHIPELAGO, CHILE: ECOLOGICAL AND HISTORICAL FACTORS WITH IMPLICATIONS FOR CONSERVATION[1]

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The level and apportionment of allozyme diversity were determined for 29 endemic (and 1 native) species from the Juan Fernández Islands, Chile. Mean diversities at the species level ($H_{es} = 0.065$) are low but comparable to those measured for other insular endemics in the Pacific. A high mean proportion (0.338) of species-level diversity resides among populations. Diversity statistics were compared for species in different ecological–life history trait categories and abundance classes. Species occurring in large populations and those present in scattered small populations have higher diversities than species occurring in one or two populations. Although not significant with the conservative statistical test employed, lower diversity was found in highly selfing species as compared to animal- or wind-pollinated species. The apportionment of genetic diversity within and among populations (G_{ST} values) is not significantly different for any of the species categories. Of particular interest is the lack of difference between animal- and wind-pollinated species because previous analyses of large data sets showed higher differentiation between populations of animal- than wind-pollinated species. Historical factors, both ecological and phylogenetic in nature, can influence the level and apportionment of diversity within insular endemics, and thus ecological correlates of diversity seen in many continental species may not apply to endemics. The results have several conservation implications. The preservation of large populations or several small populations is important for conserving diversity within species because when species are reduced to one or two populations, allozyme diversity is sharply reduced. High mean G_{ST} values for the species examined illustrate the need for conserving as many populations as possible, either in the wild or in the garden, to preserve maximal diversity within species. Effective conservation strategies require empirical knowledge of each species.

Key words: allozymes; conservation; genetic variation; Juan Fernández Archipelago; rare species.

Plants endemic to oceanic islands represent some of the most fascinating products of the evolutionary process found anywhere on earth (Carlquist, 1974). The endemic floras of oceanic islands are being lost at a higher rate than continental species (Reid and Miller, 1989; Smith et al., 1993), and therefore it is urgent that these plants be preserved (Carlquist, 1998; Raven, 1998). In addition to the inherent value of preserving insular endemics as part of our natural heritage, island plants are attractive model organisms for the study of plant speciation and evolution (Crawford, Whitkus, and Stuessy, 1987; Crawford and Stuessy, 1997; Baldwin et al., 1998).

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Species on oceanic islands often occur in very few small populations, and while many extinctions of insular species are the result of the direct or indirect negative impact of humans (Olson, 1989; Cronk, 1997; Maunder, Culham, and Hankamer, 1998; Raven, 1998; Stuessy, Crawford, and Silva O., 1998; Stuessy et al., 1998a), lack of genetic diversity associated with small population sizes is also a contributing factor in extinctions (Frankham, 1997).

Enzyme electrophoresis has been widely used to assess genetic diversity within and among populations of plant species (Hamrick and Godt, 1989), and insular endemic plant species have been examined for allozyme diversity by de Joode and Wendel (1992) and Francisco-Ortega et al. (2000). These two reviews show low diversity in insular endemics and suggest that there is lower variation within species of Pacific island endemics (de Joode and Wendel, 1992) than in Canary Island endemics (Francisco-Ortega et al., 2000). Low diversity has been attributed to a variety of factors, including bottlenecks associated both with establishment of colonizing ancestors on the island and the founding of new populations (either with or without subsequent speciation), and inbreeding and drift in

small populations (Barrett and Kohn, 1991; de Joode and Wendel, 1992; Ellstrand and Elam, 1993). The other generalization emerging from allozyme studies of island species is the high proportion of diversity residing among populations (de Joode and Wendel, 1992; Francisco-Ortega et al., 2000).

Hamrick and collaborators (Hamrick, Linhart, and Mitton, 1979; Loveless and Hamrick, 1984; Hamrick, 1989; Hamrick and Godt, 1989, 1996, 1997) provided extensive analyses of the correlation between selected ecological attributes of species and the level and apportionment of allozyme diversity within and between populations. There have been, to our knowledge, no concerted attempts to systematically classify insular endemic species into different ecological trait categories or to group them according to number, size, and distribution of populations and then compare the level and apportionment of diversity for taxa in the different groups. The review by Francisco-Ortega et al. (2000) did, however, provide some comments and analyses of genetic variation in Canary Island species, although the intensity of sampling and the different arrays of enzymes assayed in the different studies limited the generalizations that could be made. It would be of conservation value to know whether the generalizations for plants as a whole apply to insular endemics. For example, if selfing species in general have higher allozyme differentiation between populations than outcrossed wind pollinated species, initial conservation strategies would differ for the two types of species. If, however, such generalizations do not apply to insular endemics, then breeding systems would not be a useful initial guide for preserving maximum genetic diversity. Also, even if only the apportionment of allozyme diversity between populations of a species were known, the information in and of itself could be useful as an initial guide for conservation, even if reproductive biology or other ecological traits are not known.

Several of the aforementioned factors, such as drift in small populations and bottlenecks associated with both colonization and subsequent radiation and speciation, could outweigh ecological features in determining the level and apportionment of species diversity. In addition, rapid and recent evolution (such as change in breeding system) in the island setting without sufficient time for ''adjustments'' in the level and pattern of allozyme diversity could produce results differing from generalizations in the literature. Given that morphologically and ecologically divergent congeneric species on oceanic islands may exhibit minimal if any divergence at allozyme loci (e.g., Helenurn and Ganders, 1985; Lowrey and Crawford, 1985; Witter and Carr, 1988; Francisco-Ortega et al., 1992, 1996), it would not be surprising if a similar decoupling occurs between ecological features and patterns of allozyme diversity.

The Juan Fernández (Robinson Crusoe) Islands are located some 650 km west of continental Chile at ~33° S latitude. The two major islands are Masatierra (Isla Róbinson Crusoe), which is nearer the continent, 48 km^2 in size, and some 4.0 million years old (mya); and Masafuera (Isla Alejandro Selkirk), which is 150 km farther west, 50 km^2 in area, and 1–2.4 mya (Stuessy et al., 1984; Stuessy, 1995). The small island (2.2 km^2) of Santa Clara is 1.0 km to the southwest of Masatierra. The total vascular flora of the archipelago consists of 436 species, with >50% of them introduced (Swenson et al., 1997). Among the native and endemic vascular plants there are 100 endemic species of flowering plants, and it is estimated that ~80% of the endemic species are threatened (Reid and Miller, 1989).

In the present paper, we bring together allozyme data for 29 (Table 1) of the 100 endemic species (plus one native species) of flowering plants on the Juan Fernández and compare diversity statistics for taxa with different population sizes and numbers and various life history traits. The results are compared to those reported by Hamrick and Godt (1989, 1996, 1997) for plants in general and, whenever possible, with the results of Francisco-Ortega et al. (2000).

MATERIALS AND METHODS

The species and numbers of populations examined are given in Table 1; a complete list of populations is available at the *AJB* Supplementary Data web site (http://ajbsupp.botany.org/). For most species, sampling was from populations throughout their known distribution ranges. In nearly all cases when one or two populations were sampled, they represent the only ones known for the species. For populations consisting of fewer than 25 individuals, all plants were usually sampled; for larger populations, 25–30 individuals (rarely fewer than 20) were usually examined.

The allozyme data were gathered during the past decade, with results (or partial results) for some taxa reported in prior papers. However, the results reported in Table 1 represent first reports for 12 of the 30 species, and updated calculations based on more extensive population sampling are given for 9 other species (Table 1). Sources of enzymes included plants grown from seed collected in the islands, plants collected in the islands and kept at 4°C until returned to the laboratory at Ohio State, and fresh plant material in which electrophoresis was carried out on Masatierra island within 24 h of collection. All populations of 12 species were analyzed on Masatierra during expeditions in January 1996 and 1997. For selected species, banding patterns were compared for plants grown from seed, those collected in the islands and run at Ohio State, and individuals analyzed on Masatierra. In all instances, the patterns were identical, or the same variation detected from one plant source was seen in another.

The extraction buffer consisted of 0.1 mol/L tris-HCl (pH 7.5), 14 mmol/L 2-mercaptoethanol, 1 mmol/L EDTA (tetrasodium salt), 10 mmol/L $MgCl_2$, 10 mmol/L KCl, 10% glycerol (if polyacrylamide gel electrophoresis was used), and 5–10 mg polyvinylpolypyrrolidone per buffer (Gottlieb, 1981). The two buffer systems used with 12% starch gels were: (1) electrode buffer of 0.5 mol/L tris, 0.65 mol/L boric acid, 10 mmol/L EDTA, pH 8.0, and this was diluted 1 : 9 for the gel buffer; and (2) electrode buffer of 40 mmol/L citric acid titrated to pH 6.1 with N-(3-aminopropyl)-morpholine, with the gel buffer at a 1 : 19 dilution. For polyacrylamide discontinuous gel electrophoresis, a 6.0% running gel (0.375 mol/L tris-HCl, pH 8.9) and a 3% spacer gel (0.06 mol/L tris-HCl, pH 6.7) were employed together with an electrode buffer of 0.005 mol/L tris-0.038 mol/L glycine, pH 8.3 (Davis, 1964).

Enzymes resolved in starch gels with the tris-EDTA-borate buffer system were glucose-6-phosphate isomerase (GPI, EC [Enzyme Commission] 5.3.1.9), phosphoglucomutase (PGM, EC 5.4.2.2), triose-phosphate isomerase (TPI, EC 5.3.1.1), and aminopeptidase (AMP, EC 3.4.11.1). Enzymes run with the morpholine-citrate buffer system were isocitrate dehydrogenase (IDH, NADP form, EC 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.17), phosphogluconate dehydrogenase (PGD, EC 1.1.1.44); and shikimate dehydrogenase (SKDH, EC 1.1.1.2). Enzymes resolved in polyacrylamide gels were alcohol dehydrogenase (ADH, EC 1.1.1.1) and glutamate dehydrogenase (GDH, EC 1.4.1.2). Staining protocols followed Wendel and Weeden (1989).

The known active subunit composition of enzymes and observed patterns of variation within and between populations were used to infer the genetic bases of the banding patterns. Another kind of evidence examined was the minimal number of isozymes expected for diploid plants (Weeden and Wendel, 1989); chromosome numbers are known for >20 of the species (Sanders, Stuessy, and Rodríguez, 1983; Spooner et al., 1987; Sun, Stuessy, and Crawford, 1990), and ploidy levels could be inferred from this information. For certain genera such as *Dendrosersis*, chloroplast enrichment identified the plastid forms of several enzymes, thus further facilitating genetic inference (Crawford et al., 1987). Allelic frequencies were determined for each population and gene diversity statistics (Nei, 1973) calculated for each species

TABLE 1. Gene diversity statistics for 30 species of plants in the Juan Fernandez Islands. Dashes indicate that G_{ST} (proportion of species diversity occurring among populations) could not be calculated because there was no diversity within the species or only one population was sampled.

Taxon	No. populations studied[h]	P_p	H_{es}	H_{ep}	G_{ST}
Asteraceae					
Centaurodendron dracaenoides Johow[a]	2[h]	0.06	0.007	0.006	0.049
Dendroseris berteroana (Dcne.) Hook & Arn.[b]	6	0.00	0.000	0.00	—
D. litoralis Skottsb.[b]	3[h]	0.14	0.071	0.006	0.745
D. micrantha (Bertero & Dcne.) Hook. & Arn.[b]	3	0.14	0.065	0.015	0.809
D. neriifolia (Dcne.) Hook. & Arn.[b]	2[h]	0.05	0.053	0.000	1.000
D. pinnata (Bertero ex Dcne.) Hook. & Arn.[b]	4	0.05	0.029	0.010	0.733
D. pruinata (Johow) Skottsb.[b]	3	0.00	0.000	0.000	—
Erigeron fernandezianus (Colla) Harling[a]	15	0.22	0.069	0.052	0.294
Robinsonia evenia Phil.[c]	9	0.41	0.092	0.067	0.310
R. gayana Dcne.[c]	15	0.72	0.181	0.121	0.395
R. gracilis Dcne.[c]	6	0.71	0.281	0.184	0.207
R. thurifera Dcne.[c]	4	0.07	0.033	0.033	0.000
Berberidaceae					
Berberis corymbosa Hook. & Arn.[a]	2	0.40	0.148	0.101	0.333
Campanulaceae					
Wahlenbergia berteroi Hook. & Arn.[d]	2	0.00	0.000	0.00	—
W. fernandeziana Dcne.[d]	3	0.42	0.156	0.145	0.176
W. masafuerae (Phil.) Skottsb.[d]	2	0.00	0.000	0.00	—
Chenopodiaceae					
Chenopodium crusoeanum Skottsb.[a]	2[h]	0.00	0.000	0.00	—
C. sanctae-clarae Johow[e]	1	0.00	0.000	0.00	—
Euphorbiace					
Dysospsis hirsuta Mull. Arg.[a]	21	0.30	0.039	0.022	0.299
Fabaceae					
Sophora fernandeziana (Phil.) Skottsb.[a]	5	0.19	0.038	0.022	0.351
Halorrhagidaceae					
Halorrhagis masatierrana Skottsb.[a]	7	0.33	0.074	0.066	0.121
Lactoridaceae					
Lactoris fernandeziana Phil.[f]	12	0.00	0.000	0.000	—
Lamiaceae					
Cuminia eriantha Benth.[a]	10	0.37	0.111	0.083	0.262
Myrtaceae					
Myrceugenia fernandeziana (H. & A.) Berg.[a]	19	0.67	0.091	0.056	0.232
Piperaceae					
Peperomia berteroana Miq.[a]	6	0.39	0.178	0.136	0.244
P. margaritifera Hook.[a]	1[h]	0.05	0.017	0.017	—
P. fernandeziana Miq.[a]	3	0.09	0.056	0.046	0.182
Rutaceae					
Fagara mayu (Bert.) Engl.[a]	15	0.38	0.076	0.044	0.406
Solanceae					
Solanum fernandezianum Phil.[a]	2	0.00	0.000	0.00	—
Verbenaceae					
Rhapithamnus venustus (Phil.) Skottsb.[g]	14	0.17	0.028	0.022	0.224

[a] First report for species or given in de Joode and Wendel (1992) based on fewer population samples.
[b] Crawford et al. (1998).
[c] Includes populations in addition to those reported in Crawford et al. (1992).
[d] Crawford et al. (1990).
[e] Crawford, Skeussy, and Silva O. (1988).
[f] Crawford et al. (1994).
[g] Crawford et al. (1993).
[h] Designates species known from fewer than 25 individuals in the wild.

using a modified version of Gene Stat-pc, version 3.3 (Lewis, 1993). For each species, species level diversity (H_{es} of Hamrick and Godt, 1989) and mean population diversity (H_{ep}) were calculated. The proportion species diversity residing among populations (G_{ST}) was determined by calculating G_{ST} for all polymorphic loci and then averaging over the loci (Hamrick and Godt, 1989). The proportion polymorphic loci was calculated for each species; a locus was defined as polymorphic if the most common allele was present in a frequency of 0.99 or less in a species.

Ten categories, including those selected from Hamrick and Godt (1989), were established, and gene diversity statistics compared for the different groups (Table 2). These include three categories of population size and number, three based on life form, and four based on aspects of the breeding system (Table 2). Because of small sample sizes and non-normal distributions for the genetic diversity estimates, the Mann-Whitney test was used to evaluate between-group differences (Table 3). Given that the groups involved in each comparison are simply subsets of the same samples, the sequential Bonferroni technique (Rice, 1988) was used to maintain an experiment-wise error rate of 0.05 for each set of comparisons (four sets corresponding to the four measures of diversity). In addition, some comparisons were evaluated as two-tailed tests, while others were evaluated as one-tailed tests.

RESULTS

The number of loci resolved per species ranged from 12 to 24, although not every locus was scored in every individual

TABLE 2. Means and ranges (in parentheses) of diversity statistics for species in different categories. Dashes indicate that G_{ST} (proportion of species diversity occurring among populations) could not be calculated because for most or all species in one or both categories there was no diversity within the species or only one population was sampled.

Category	No. species	P_p	H_{es}	H_{ep}	G_{ST}
Large populations (2 or more populations with >100 individuals)	7	0.44 (0.30–0.72)	0.117 (0.002–0.281)	0.081 (0.000–0.184)	0.255 (0.071–0.438)
Small, scattered populations (10 or more populations with ≤5 plants)	8	0.19 (0.00–0.40)	0.072 (0.000–0.148)	0.048 (0.000–0.095)	0.385 (0.000–0.809)
One or two known populations	6	0.02 (0.00–0.06)	0.013 (0.000–0.053)	0.001 (0.000–0.006)	—
Dioecious species	6	0.40 (0.07–0.72)	0.127 (0.033–0.281)	0.090 (0.033–0.184)	0.247 (0.000–0.406)
Wind-pollinated species	8	0.45 (0.07–0.72)	0.107 (0.033–0.281)	0.074 (0.022–0.184)	0.238 (0.000–0.406)
Insect/bird-pollinated species	4	0.22 (0.16–0.37)	0.073 (0.33–0.115)	0.055 (0.022–0.095)	0.245 (0.172–0.428)
Highly or obligately selfing	6	0.12 (0.00–0.42)	0.026 (0.000–0.156)	0.024 (0.000–0.145)	—
Long-lived woody	7	0.33 (0.16–0.40)	0.086 (0.028–0.115)	0.056 (0.022–0.095)	0.278 (0.152–0.406)
Short-lived woody	11	0.23 (0.00–0.42)	0.059 (0.000–0.281)	0.048 (0.000–0.184)	0.386 (0.000–1.000)
Long-lived perennial herbs	10	0.18 (0.00–0.42)	0.059 (0.000–0.178)	0.048 (0.000–0.136)	0.186 (0.121–0.294)

because of low activity and/or resolution. For the majority of species, 15–20 loci were analyzed. The same ''core'' array of enzymes (AMP, GPI, IDH, MDH, PGD, PGM, TPI) was scored in nearly all populations, so variation among populations and species was not an artifact of the loci sampled. The proportion of polymorphic loci (P_p) within species ranged between 0.00 and 0.72, with a mean of 0.21 (Table 1). Total diversity (H_{es}) within species varied from 0.000 (several species) to 0.281 in *Robinsonia gracilis* (Table 1); the mean total diversity for all species was 0.065. The mean populational diversity (H_{ep}) varied from 0.000 (several species) to 0.184 in *Robinsonia gracilis* (Table 1), with an average of 0.044 for all samples. The G_{ST} values ranged from 0.000 to 1.000, with an average of 0.338 for all species for which they could be calculated (i.e., more than one population examined and some allozyme diversity detected).

The means and ranges for P_p, H_{es}, H_{ep}, and G_{ST} for the different species groups are given in Table 2. Mean values for P_p ranged from 0.02 for species known from one or two populations to 0.44 for species occurring in large populations. Mean total species diversity (H_{es}) varied from 0.013 for species existing in one or two populations to 0.127 for dioecious species, and the same two groups had the lowest and highest populations diversities (H_{ep}). Mean G_{ST} values were lowest for long-lived perennial herbs and highest for short-lived woody species and for species occurring in small scattered populations (Table 2). The levels of significance (P values) for the Mann-Whitney tests between the groups are shown in Table 3. Values

TABLE 3. P values from Mann-Whitney tests between specific subsets of taxa (all tests evaluated as two-tailed tests except as noted). Values with asterisks are significant at an experiment-wise $P = 0.05$ (see text for explanation). Dashes indicate that G_{ST} (proportion of species diversity occurring among populations) could not be calculated because for most or all species in one or both categories there was no diversity within the species or only one population was sampled.

Comparison	H_{es}	H_{ep}	P_p	G_{ST}
Species with large vs. one or two populations[a]	0.002*	0.001*	0.001*	—
Species with small, scattered vs. one or two populations[b]	0.018	0.014	0.002*	—
Species with large vs. small, scattered populations[c]	0.178	0.055	0.048	0.100
Dioecious vs. all other species except selfers	0.005	0.021	0.025	1.000
Selfers vs. wind-pollinated species[d]	0.018	0.013	0.009	—
Insect/bird- vs. Wind-pollinated species	0.307	0.303	0.102	0.838
Long-lived woody vs. perennial herbs	0.278	0.445	0.104	0.109
Long-lived trees vs. palmiform short-lived trees	0.365	0.130	0.108	0.554
Species with large populations vs. all other species[e]	0.005	0.004*	0.001*	0.551
Insect/bird- and wind-pollinated vs. selfing species[f]	0.022	0.008	0.011	—
Species in large populations vs. all other species except selfers[g]	0.007	0.006	0.002*	0.721
Dioecious vs. all other species	0.010	0.016	0.014	0.916

[a] One-tailed tests; H_A = large > 1 or 2.
[b] One-tailed tests; H_A = small, scattered > 1 or 2.
[c] H_{ep} and G_{ST} one-tailed; H_A = small, scattered > large.
[d] One-tailed test; H_A = wind-pollinated species > selfers.
[e] One-tailed tests; H_A = large > all others.
[f] One-tailed tests; H_A = Insect/bird-, wind-pollinated species > selfers.
[g] One-tailed tests; H_A = large > all others except selfers.

using the sequential Bonferroni technique were significantly different (experiment-wise $P = 0.05$) for H_{es}, H_{ep}, and P_p between species with large populations and those occurring in one or two populations. In addition, P_p values were significantly higher for species in small scattered populations than for those occurring in one or two populations, and species in large populations have significantly higher P_p values than all other species or all other species except selfers. Lastly, species with large populations have higher H_{ep} values than all other species excluding selfers (Table 3). No significant differences in G_{ST} values were found among any of the groups (Table 3); G_{ST} comparisons could not be made for groups consisting of selfers and species known from one or two populations due to lack of allozyme diversity within species or to the fact that only one population was examined per species (Table 3).

DISCUSSION

Diversity within species and populations—Endemic plant species on average harbor less total allozyme variation than more widespread taxa, with an H_{es} of 0.096 (Hamrick and Godt, 1989, 1996); Pacific island endemics contain even lower mean diversities ($H_{es} = 0.064$) than endemics in general (de Joode and Wendel, 1992; Frankham, 1997). Factors most frequently cited include bottlenecks associated with long-distance dispersal to islands, establishment of colonizing ancestors on islands, and drift and inbreeding in small populations on the islands (de Joode and Wendel, 1992). The present survey of Juan Fernández endemics revealed mean species level diversity nearly identical to the mean value de Joode and Wendel (1992) reported for species endemic to Pacific islands. The range of values ($H_{es} = 0.000$–0.281) in this study exceeds the range ($H_{es} = 0.000$–0.195) reported in the review of de Joode and Wendel (1992). More recent studies of allozyme diversity in 69 species of Canary Island endemics revealed considerably higher ($H_{es} = 0.186$) mean total diversity (reviewed by Francisco-Ortega et al., 2000), but with a wide range of values (e.g., Morikawa and Leggett, 1990; Francisco-Ortega et al. 1992, 1996; Charmet and Balfourier, 1994; Borgen, 1996; Kim et al., 1999) for species. One possible hypothesis for higher diversities in the Canary Island endemics is that some species are old lineages that survived glaciations and desertification in Europe and northern Africa after the Miocene (Francisco-Ortega et al., 2000). This hypothesis is rendered more plausible by the older ages of some Canary Islands (>20 million years) relative to ages of <5 million years for most Pacific islands, as mutations at allozyme loci through time would increase diversity (Witter and Carr, 1988). Francisco-Ortega et al. (2000) emphasized, however, that phylogenetic (particularly molecular-phylogenetic) studies for several Canary Island groups show them to be highly derived lineages. The close proximity of the Canaries to continental areas (compared to Pacific archipelagos such as Hawaii, Galápagos, and Juan Fernández) increases the probability of multiple introductions, which could alleviate genetic bottlenecks associated with founder events and result in higher genetic diversity. However, molecular phylogenetic studies for several groups suggest that even the most diverse island lineages are the result of single introductions (Francisco-Ortego et al., 2000). Higher incidence of interspecific hybridization could account for higher allozyme diversity in Canary Island endemics, as hybridization has been documented for several groups (Francisco-Ortega et al., 2000). In contrast, interspecific hybridization is rare in the Juan Fernández Islands and other Pacific archipelagos (Stuessy, Crawford, and Silva O., 1998). Additional studies are needed to elucidate the factors responsible for higher mean allozyme diversity in Canary Island endemics as compared to species of Pacific islands.

Breeding system has been shown to be one of the most important life history factors in explaining allozyme diversity within species and the apportionment of the diversity among populations of species (Hamrick and Godt, 1996). Using the rather conservative sequential Bonferroni analysis, no significant differences were found between wind-pollinated (largely outcrossing) species and highly selfing species for any of the diversity measures. If both wind- and insect/bird-pollinated species are combined and compared to selfing species, there are likewise no significant differences. However, despite the lack of significant differences with this conservative test, the lower diversity detected in selfers compared both to wind-pollinated species and to the insect/bird- and wind-pollinated species categories combined may be biologically significant, given the very low P values for these comparisons (Table 3). No differences in diversity were detected between insect/bird- and wind-pollinated species on the Juan Fernández, either at the species or population levels (Table 3); this is also true for the compilations of Hamrick and Godt (1989). Hamrick and Godt (1989) found no differences in H_{es} and H_{ep} between species with outcrossing animal, outcrossing wind, and mixed animal breeding systems, but species with mixed wind pollination had significantly higher diversities than species in the other three categories. Half of the wind-pollinated species included in this survey are highly outcrossing because they are dioecious; it is not known whether the insect/bird-pollinated species are highly outcrossing or mixed-mating. Thus, it is difficult to make precise comparisons with the results compiled by Hamrick and Godt (1989). It can be seen in Table 2 that, although mean diversities are higher in wind-pollinated than in insect/bird-pollinated species, the differences do not approach statistical significance (Table 3), even without the application of the conservative sequential Bonferroni test.

While highly selfing species have low average diversity, there is a considerable range of values among species (Table 2) within the group. Five of the six species show no allozyme variation, but one species, *Wahlenbergia fernandeziana*, has very high diversity at both the species ($H_{es} = 0.165$) and population ($H_{ep} = 0.149$) levels (Table 2). High diversity is found here despite the species being highly autogamous (Anderson et al., 2000). The wide distribution of *W. fernandeziana* on Masatierra, with some populations quite large (several hundred plants), may be a factor in maintaining high diversity. *Lactoris fernandeziana*, a species once thought to be extinct but now known from several large populations in different parts of Masatierra (Crawford et al., 1994; Stuessy et al., 1998a, b), appears to be highly geitonogamous (Bernardello et al., 1999). Despite its relative abundance, *L. fernandeziana* is like the other four species of selfers (which are very rare by comparison, with three of them known from one or two populations) in exhibiting no allozyme diversity.

The conservative sequential Bonferroni test shows that the six dioecious species included in this study do not have significantly higher diversity than either nondioecious species or nondioecious species excluding selfers (Table 3). However, dioecious taxa have about twice the average diversities (P_p, H_{es}, H_{ep}) found for all nondioecious species in the present survey (Table 2), and the low P values seen in Table 3 suggest that

the higher diversities found in dioecious species may be biologically significant. Among the dioecious taxa, two species of *Robinsonia* (*R. gayana* and *R. gracilis*) have the highest diversities of any species in this study; they also occur commonly and are often present in large populations of >100 individuals. *Cuminia eriantha,* despite occurring in very small scattered populations, has total species diversity nearly twice the mean for all species examined on Juan Fernández. Except for the very rare *Robinsonia thurifera* (discussed below), all dioecious species have diversities higher than the mean for nondioecious taxa. The processes promoting higher diversities in these species are not known, but the fact that they must outcross is likely a factor even though there could be biparental inbreeding in the smaller populations.

An important question is whether species composed of various sizes and numbers of populations have different levels of alloyzme diversity; this could be particularly relevant on the Juan Fernández, where species can differ dramatically in numbers and sizes of populations. Of the seven significant differences between groups detected with the conservative sequential Bonferroni test for evaluating *P* values, all are related to population size and number (Table 3). However, species consisting of ten or more small populations do not have significantly less diversity than those composed of large populations, even when using less conservative criteria (Table 3). Clearly, the maintenance of either large populations or ten or more small populations appears to be important in maintaining higher allozyme diversities in species of the Juan Fernández. Another clear result of this study is that when species are reduced to one or two populations there is extensive loss of diversity. Species in the Canary Islands with large populations (defined as >2500 plants) do not have significantly higher species-level diversity than species consisting of small populations (<100 plants), although the mean for the former is 0.146 (range = 0.037–0.370), while the mean for the latter is 0.097 (range = 0.000–0.360).

Apportionment of diversity within and among populations—In addition to determining levels of diversity within species and populations, knowing how diversity is apportioned within and among populations of a species is useful in formulating strategies for conserving diversity within taxa (Hamrick et al., 1991). To this end, we wished to compare species occurring in large populations with those distributed in ten or more small scattered populations. Small scattered populations may result from habitat fragmentation, and we wished to determine if there is a higher proportion of species level diversity among small scattered as compared to large populations. Processes such as drift and inbreeding in small populations and reduced gene flow among small fragmented populations promote interpopulational differentiation. Although G_{ST} values are, on average, higher for species with small scattered populations (Table 2), the difference is not significant (Table 3) even without the more restrictive sequential Bonferroni analysis.

One of the more striking results from the compilations of Hamrick and Godt (1989, 1997) is the much higher G_{ST} values found for selfers compared to outcrossing or mixed mating species. Lack of allozyme diversity in five of the six selfing species included in the present study precluded calculating G_{ST} values for species in this group. It was, however, possible to compare wind with animal-(insect/bird) pollinated species in the present study. Regardless of whether mixed mating or outcrossing species were being compared, Hamrick and Godt (1989) found significantly lower G_{ST} values for wind than animal-pollinated taxa. In contrast, for species on the Juan Fernández, no significant differences were detected between these (or any other) categories (Table 3). Thus, one of the major traits explaining apportionment of genetic diversity within and among populations of plants in the analyses of Hamrick and Godt (1989) does not hold for the Juan Fernández species. In their later analyses using two-trait categories, Hamrick and Godt (1997) did not differentiate between endemics with animal- or wind-pollinated species, but included only outcrossing, mixed-mating, and selfing species. It is noteworthy that the mean G_{ST} for Juan Fernández plants (even with the exclusion of the highly selfing species for which G_{ST} could not be calculated) is considerably higher (0.245 and 0.238 for animal and wind, respectively) than the values of 0.179 and 0.174 for mixed-mating and outcrossing endemic species, respectively (Hamrick and Godt, 1997).

The review of Francisco-Ortega et al. (2000) revealed a mean G_{ST} value of 0.281 for 23 species endemic to the Canary Islands, a value somewhat lower than the mean of 0.338 found in the present study of Juan Fernández endemics. Francisco-Ortega et al. (2000) emphasized that the species included in their calculations are outcrossers, and this could be a factor in making the G_{ST} values lower than those of Juan Fernández endemics. Still, the mean G_{ST} value for Canary Island species is higher than the mean of 0.179 for outcrossing endemic species (Hamrick and Godt, 1997). Available data indicate that, on average, there is a higher proportion of allozyme diversity among populations of Canary Island and Juan Fernández species than in endemics in general.

Historical and biological factors shaping allozyme diversity in Juan Fernández species—Hamrick and Godt (1996) opined that while generalizations from the literature can sometimes be used to predict levels and apportionment of allozyme diversity in unstudied species, the accuracy of these predictions is quite low for several ecological attributes of species. Possible reasons given for low predictability include different studies not being comparable in number of loci, sample size, and the number and spatial distribution of populations examined. It seems highly unlikely that in the present study any of these factors account for variation among species within a category or lack of differences between categories. As indicated earlier, many of the same loci were examined in all species, any large differences in sample sizes for populations reflect the number of individuals present in populations, and populations were sampled from much of the known ranges of species.

Hamrick and Godt (1996) argued that historical factors, both ecological and evolutionary, may influence the diversity now detected in a given species so that the species fails to exhibit the correlations between allozyme diversity and ecological attributes found for plants in general. Among such factors are fluctuations in the numbers and sizes of populations, biogeography, and the process of speciation. These factors, as well as others, could be particularly strong in the insular setting, where populations are often small and scattered and speciation is rapid. In Juan Fernández endemics, there are, as indicated above, examples in which generalizations found for plants as a whole do not hold because of the large range of variation among species within categories.

In several instances where taxa have been studied in some

detail, it has been possible to formulate feasible hypotheses for observed levels and apportionment of allozyme diversities. For example, within the genus *Robinsonia,* there is a wide range of gene diversities among the species, and it may be seen in Table 1 that *R. gayana* has well over five times the total diversity of *R. thurifera.* Phylogenies for the genus based on morphological characters (Sanders et al., 1987) and ITS sequences (Sang et al., 1995) place the two species as the only members of a strongly supported clade. *Robinsonia thurifera* is a very rare species and likely represents a recent derivative (perhaps originating as a peripheral population) of *R. gayana* or of a common ancestor of the two species (Crawford et al., 1998). A reasonable hypothesis is that *R. thurifera* is in a severe bottleneck associated with its recent origin and this historical factor, rather than ecological trait differences, explains its very low allozyme diversity compared to its sister species.

Dendroseris litoralis represents another possible example where level of allozyme diversity reflects historical rather than ecological causes. The species has more total diversity (H_{es} = 0.071; Table 1) than might be expected given that it is now known from only two small natural populations on Santa Clara and two small rocks on the coast of Masatierra (Stuessy et al., 1998a, b). Also, the species is self-compatible and perhaps highly selfing, although still visited by hummingbirds (Anderson et al., 2001). The species was once common on the coast of Masatierra around the town of San Juan Bautista, but it now survives almost totally as a common street tree in the village. Despite being highly selfing, pollen-ovule ratios for *Dendroseris litoralis* are indicative of an outcrosser, and the flowers produce copious nectar on which hummingbirds feed (Bernardello et al., in press). The relatively high allozyme diversity now detected (as measured from material cultivated in San Juan Bautista) may be a ''remnant'' from when the species was outcrossing and much more abundant. All species of *Dendroseris* are now quite rare (Stuessy et al., 1998a, b), but another species, *D. neriifolia,* has a total diversity of 0.053 (which is near the mean for all species examined in this study) despite being self-incompatible (Anderson et al., 2001) and known from only three plants in a badly degraded area on Masatierra (Stuessy et al., 1998a, b). There is little question that *D. neriifolia* was once more abundant (Skottsberg, 1922) and, as with *D. litoralis,* this may account for the higher diversity than would be expected in such a rare species. By contrast, *D. berteroana,* in which no allozyme diversity was detected despite extensive sampling, occurs in small isolated populations at high (and highly inaccessible) elevations where there has been minimal, if any, human disturbance. It may be that these populations have always been small and the lack of allozyme diversity is a reflection of the history of this species.

The variation in genetic diversity among species within single-trait categories and the concomitant lack of significantly different mean genetic diversities between categories are to some extent reflections of the limitations of comparisons based on single traits. These limitations may be especially pronounced for insular taxa, where recent speciation, rapid evolution, and stochastic processes such as drift may be more important influences on genetic diversity than traits used to erect the categories. Several cases cited above are examples of these situations.

The mean proportion of total species diversity existing among populations is high (G_{ST} = 0.338) compared to the compilations of Hamrick and Godt (1997) for endemics, despite only two selfing species being included in the present survey. The mean for Juan Fernández plants is nearly twice as high as values for mixed mating or outcrossed endemics, and the mean is also >35% higher than for endemics as a whole (Hamrick and Godt, 1989). While on average a relatively large proportion of allozyme diversity resides among populations of Juan Fernández endemics, comparison of G_{ST} values for different categories of endemics produced unexpected results compared to generalizations in the literature, one of them being the aforementioned lack of difference between wind- and insect/bird-pollinated species on the island. On the Juan Fernández, this could be the result of wind and animals being about equally effective (or ineffective) in dispersing pollen between small isolated populations in the islands. Hummingbirds are the primary animal pollinators on Juan Fernández (Anderson et al., 2001) and they may, on average, disperse pollen as efficiently as wind. However, within each of the pollinator categories there exists a wide range of G_{ST} values, and it is difficult to account for them on the basis of available ecological or other information. An example is afforded by *Rhaphithamnus venustus* and *Sophora fernandeziana,* each of which is hummingbird pollinated (Anderson et al., 2001) and occurs primarily as small scattered populations. However, the former species has a G_{ST} of 0.234 while the value for the latter species is >50% higher (Table 1). One possible explanation for this difference is that *R. venustus* is more common and widely distributed than *S. fernandeziana* on Masatierra and larger populations of the former species are rarely found. Thus, drift may have a more pronounced effect in the smaller populations of *Sophora. Rhaphithamnus venustus* occurs at higher elevations than *S. fernandeziana,* and it may be easier for pollen to be transported between populations in different canyons. An alternative, but not mutually exclusive, explanation is that *Rhaphithamnus* was once much more abundant and continuously distributed on Masatierra than it is at present or than *Sophora* has ever been. The low differentiation among the populations of *R. venustus* may be a remnant of its former distribution. There are no apparent ecological factors accounting for the different G_{ST} values for the two species, and it must be admitted that the possible historical factors presented above are highly speculative.

Conservation implications—Mean allozyme diversity is low in species of the Juan Fernández islands, and it is comparable to the value given in an earlier compilation for Pacific insular endemics (de Joode and Wendel, 1992). Those species in Juan Fernández occurring in large populations (>100 plants), or present in ten or more small (as few as five individuals) populations have significantly higher diversity than species known from one or two populations. The maintenance of species diversity is dependent on species occurring either in large populations or in small scattered populations. When species become reduced to one or two populations, species level diversity decreases sharply. Although not appearing significantly different with the conservative analyses used in this study, highly selfing species have much lower average diversity (highly significant *P* values in the Mann-Whitney test; Table 3) than species that are either or animal or wind pollinated. Therefore, selfing species appear to be especially vulnerable if allozymes are a reasonable indicator of genetic diversity within species.

Hamrick et al. (1991) emphasized the importance of knowing the distribution of genetic variation within a species for designing strategies for preserving genetic diversity. In the

present study, G_{ST} was employed to assess apportionment of diversity within and among populations of species, and two results are important relative to conservation. First, on average the proportion of diversity among populations (0.338) is quite high (cf. Hamrick and Godt, 1989). This mean value does not include most selfing species because they totally lack allozyme diversity, and if selfing species could have been included, the mean value would have likely been higher given the very high G_{ST} values typically found in selfers (Hamrick and Godt, 1989). There are ongoing efforts to conserve the rarest species in the Juan Fernández by cultivating them in the CONAF garden in San Juan Bautista, followed by reintroduction into the wild. The high mean G_{ST} values suggest that congeneric populations could differ in ecological attributes or other characters adaptive to the localized disjunct areas where they now occur on Masatierra. This means that the source areas of plants cultivated in the garden should be documented so that reintroduction can be made into the original habitats. Congeneric insular endemic species are often highly interfertile (Crawford and Stuessy, 1997; Francisco-Ortega et al., 2000), thus conservation by cultivation in the garden must be done with caution to prevent interspecific hybridization, and this is particularly true for wind-pollinated species, which are common on the Juan Fernández (Anderson et al., 2001).

This study also revealed that G_{ST} values do not differ significantly for any of the species categories. Hamrick and Godt (1989) showed from their analyses of available data that animal-pollinated species have lower G_{ST} values than wind-pollinated taxa, but this difference was not detected between these two groups in the Juan Fernández. Also, one might expect that species in large populations would have a lower level of differentiation than those occurring in small scattered populations because the smaller populations could become differentiated by drift and inbreeding, and gene flow could be lower among them than among larger populations. In the Juan Fernández, by contrast, one cannot make assumptions about apportionment of allozyme diversity based on pollination biology and size and distributions of populations. As emphasized by Hamrick and 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. Based on results of the present study, the most effective conservation strategies for given species can be developed only after both historical and ecological information is available for them.

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