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GENETIC DIVERSITY IN *DELPHINIUM VARIEGATUM* (RANUNCULACEAE): A COMPARISON OF TWO INSULAR ENDEMIC SUBSPECIES AND THEIR WIDESPREAD MAINLAND RELATIVE[1]

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Delphinium variegatum is subdivided into three subspecies: *D. v. variegatum* is widespread in central and northern California, while *D. v. kinkiense* (an endangered taxon) and *D. v. thornei* are endemic to San Clemente Island off the coast of southern California. Electrophoretic data for 19 loci were collected from 7 populations of the mainland subspecies and all 24 known populations of the two insular endemic subspecies. Populations of the widespread mainland subspecies have more polymorphic loci (33.6% vs. 24.5%) and more alleles per polymorphic locus (2.61 vs. 2.15) than the insular endemic subspecies. However, observed heterozygosities are lower in the mainland subspecies (0.041 vs. 0.071), presumably due to lower levels of outcrossing ($t = 0.464$ vs. 0.895). Expected heterozygosities are similar (0.064 vs. 0.074) due to lower alternative allele frequencies in populations of the mainland subspecies (mean $q = 0.075$ vs. 0.190). Populations of the two insular subspecies are almost equivalent genetically (mean $I = 0.997$) regardless of taxonomic designation or geographic location. In contrast, one of the mainland populations is genetically well differentiated from the others. If this exceptional population is excluded, the mainland subspecies partitions genetic diversity similarly to the island subspecies, with most variation being found within populations ($G_{ST} = 0.073$ vs. 0.030).

Key words: allozymes; conservation; *Delphinium*; endangered species; endemic; genetic diversity; Ranunculaceae; San Clemente Island.

Increased extinction of rare and endangered species has led to concern for the viability of many plants and animals and heightened the need for more successful conservation efforts. Because rare species face an increasingly uncertain future, many studies have attempted to identify features characterizing rare species (Baskauf, McCauley, and Eickmeier, 1994). Genetic aspects of rarity have received attention because the long-term survival of a species depends not only on habitat and demographic factors but is ultimately linked to the genetic diversity available to a species. Genetic diversity is required for maintaining evolutionary potential in a changing environment (Holsinger and Gottlieb, 1991; Ellstrand and Elam, 1993). Rare and endemic species have been expected to have depleted levels of genetic variation due to genetic drift in small populations and strong directional selection leading to genetic uniformity in a limited array of environments (Wright, 1931; Van Valen, 1965; Babbel and Selander, 1974; Nei, Maruyama, and Chakraborty, 1975; Franklin, 1980; Barrett and Kohn, 1991).

Studies of genetic variation in plant species have revealed a strong association between the level of genetic diversity in a species and its geographic range (Hamrick and Godt, 1989). In general, wide-ranging species maintain considerably higher levels of genetic diversity, both at the population and species levels, presumably because of isolation of populations or diversifying selective forces across the range (Baskauf, McCauley, and Eickmeier, 1994). However, results of studies on the genetic structure of rare and endemic plants are far from homogeneous. Not all rare and endemic plant species are genetically depauperate, and some rare species have levels of genetic variation higher than those found in widespread species (e.g., Nickrent and Wiens, 1989). Clearly, many other factors, such as the nature of the speciation process, life-history traits, and the recent history of population fluctuations, may affect the amount and distribution of genetic variation in plant species (Karron, 1987). Moreover, different studies use nonidentical sets of genes to assay genetic variability, providing a methodological cause for differences in observed patterns of genetic variation in addition to biological factors.

Kruckeberg and Rabinowitz (1985) recommended comparative study of rare taxa and related common taxa. Closely related species are likely to share many life-history features due to recent common ancestry, making it easier to identify the causes of differences in genetic diversity. Karron (1987) evaluated the correlation between genetic variation and geographic range for 11 pairs of congeneric species and found that geographically restricted species have significantly lower levels of genetic variation than their widespread relatives.

Gitzendanner and Soltis (2000) reviewed 34 subsequent studies of genetic variation in pairs of rare and widespread congeners. They found only small, but significant, differences for most measures of genetic diversity, but no differences in the partitioning of genetic variation within and among populations. Measures of diversity were highly correlated between rare and widespread congeners, demonstrating both the importance of factors other than rarity and the need to conduct comparisons of related species. However, the studies that were

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reviewed addressed situations that are diverse with respect to evolutionary history and to the components of rarity (geographic range, habitat specificity, and population size; Rabinowitz, 1981). In some, the rare species is a habitat specialist in addition to having a narrower distribution (e.g., Baskauf, McCauley, and Eickmeier, 1994), while in others, the rare species is characterized by smaller population sizes (e.g., Crawford et al., 1992). In yet others, habitat specificity and population sizes of the congeners are not reported (e.g., Cole and Biesboer, 1992). An additional confounding factor in some studies is that the widespread and geographically restricted species may be a progenitor-derivative pair (e.g., Pleasants and Wendel, 1989; Linhart and Premoli, 1993; Kadereit et al., 1995). Thus, the association of specific components of rarity, such as geographic range, with levels of genetic variation is still not adequately known.

It is unlikely that the effects of geographic range, habitat specificity, and population size can be completely isolated from each other in studies of natural populations. Current levels of genetic variation are partly determined by past population sizes, which are usually unknown. However, the effects of geographic range and habitat specificity can be separated, and additional data regarding their association with genetic variation in closely related taxa continue to be of interest, especially in cases where information regarding past population sizes is available.

This study investigates the association between genetic diversity and geographic range using the three subspecies of *Delphinium variegatum*, which occupy similar habitats, have similar life history traits, and currently have similar population sizes. One subspecies is widespread in mainland California, while the other two are insular endemics found only on the adjacent San Clemente Island. One of the insular endemic subspecies is endangered, and the study was initiated as part of an investigation of the conservation genetics of rare and endangered plant species of San Clemente Island. The specific goals of the study were to (1) assess the genetic diversity of the geographically restricted insular subspecies in relation to their widespread mainland relative, (2) evaluate the distinctness of the insular subspecies, and (3) provide management guidelines for the insular subspecies based on population genetic data.

MATERIALS AND METHODS

Study species—*Delphinium variegatum* Torrey & A. Gray (Ranunculaceae) is a perennial larkspur that is found in grassland and open woodlands of mainland California and San Clemente Island, the southernmost of the Channel Islands off the coast of southern California, USA (Warnock, 1990b). One subspecies, *D. v.* subsp. *variegatum* (Royal larkspur), is found exclusively on the mainland and ranges approximately from northern to central California, from the coast to the foothills (Fig. 1). The other two subspecies, *D. v.* subsp. *kinkiense* (Munz) M. J. Warnock (San Clemente Island larkspur; Warnock, 1990a) and *D. v.* subsp. *thornei* (Thorne's larkspur; Munz, 1969), are insular endemics found only on San Clemente Island. The Channel Islands are thought to provide refuge for a number of species with northern affinities, including *D. variegatum* (Raven and Axelrod, 1978), that once extended farther south on the mainland during Pleistocene pluvial cycles (Raven, 1963).

The insular endemic subspecies of *D. variegatum* are vulnerable to extinction because of their rarity, endangerment, and limited distribution (Skinner and Pavlik, 1994). *Delphinium v. kinkiense* is listed as endangered by the U. S. Fish & Wildlife Service (USFWS) and by the California Department of Fish and Game. However, the rarest of the subspecies, *D. v. thornei*, has no special legal status, although the USFWS considers it to be a species of concern. Both of these taxa are on the California Native Plant Society List 1B (plants rare, threatened, or endangered in California or elsewhere; Skinner and Pavlik, 1994).

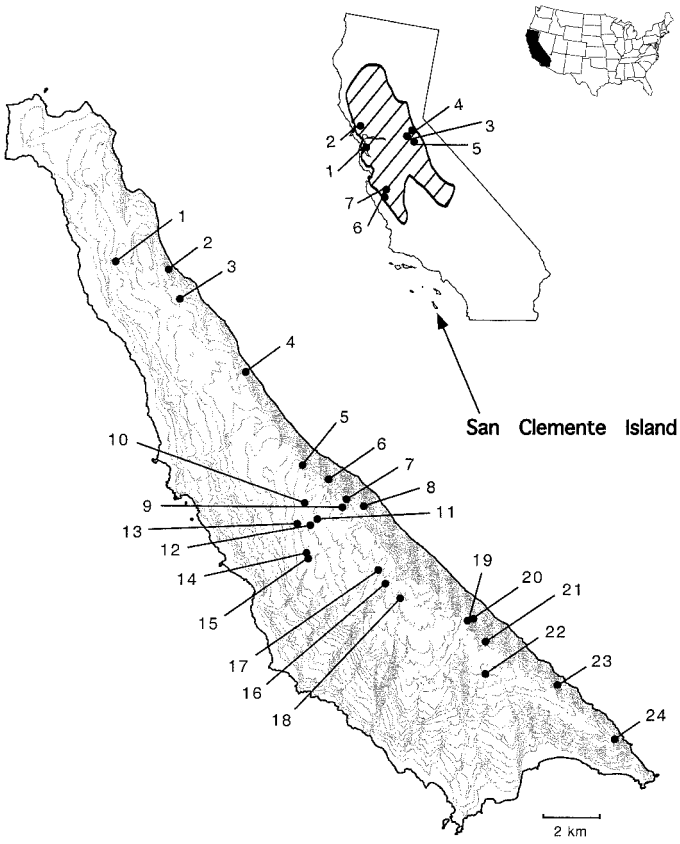

Fig. 1. Distribution and sampled populations of *Delphinium variegatum* from mainland California (subsp. *variegatum*) and from San Clemente Island (subsp. *kinkiense* and subsp. *thornei*).

The subspecies of *D. variegatum* have been distinguished primarily by three floral characters: sepal color, lateral sepal length, and lower petal blade length (Warnock, 1990b, 1993, 1997). However, there is considerable overlap among the subspecies, and intensive sampling of natural populations has shown that the two metric characters do not adequately separate any of these taxa (Dodd and Helenurm, 2000). In particular, the insular subspecies appear to be differentiated only by sepal color, with *D. v. kinkiense* having white to light blue flowers and *D. v. thornei* having light blue to bright blue flowers. *Delphinium v. kinkiense* occurs mainly in the northern part of San Clemente Island, while *D. v. thornei* occurs mainly in the southern part. Central populations often include individuals exhibiting white, bright blue, or intermediate flower colors, suggesting that hybridization may be occurring. Natural hybridization has been documented to regularly occur among other taxa in the genus *Delphinium* (Warnock, 1990b, 1997); natural hybrids are known between *D. v. variegatum* and *D hansenii*, *D. hesperium*, *D. parryi*, and *D. recurvatum* (Lewis and Epling, 1954).

Study sites—Twenty-four populations of *D. v. kinkiense* and *D. v. thornei* were located and sampled from San Clemente Island in 1996 (Fig. 1; Table 1). This represents all known populations and probably all of the populations on the island; subsequent surveys have failed to reveal additional locations (Junak and Wilken, 1998; S. Burckhalter, University of South Dakota, personal communication; K. Helenurm, personal observation). San Clemente Island has been owned by the United States Government and operated by the United States Navy since the early 1930s, providing active naval training and support activities. Historically, the island has had a long history of feral goat grazing and sheep, cattle, and pig ranching, resulting in overgrazing, subse-

TABLE 1. Population number, subspecies designation, collection locations, approximate population sizes (1996), and sample sizes of *Delphinium variegatum*. San Clemente Island populations are arranged north to south.

Population number	Subspecies	Location	Population size	Sample size
Island				
1	*kinkiense*	Flasher Canyon	200	44
2	*kinkiense*	Nots Drive	200	41
3	*kinkiense*	Pelican Canyon	2500	44
4	*kinkiense*	Larkspur Canyon	150	40
5	*kinkiense*	Stone Canyon	500	40
6	*kinkiense*	Burns-Horton Canyon	>1000	40
7	*kinkiense*	Lower Twin Dams Canyon	16	11
8	mix	Boulder	200	40
9	mix	Upper Twin Dams Canyon	1000	40
10	*kinkiense*	Warren Canyon	200	39
11	*thornei*	Upper Middle Ranch Canyon	75	40
12	mix	Lower Middle Ranch Canyon	350	40
13	*kinkiense*	Waynuk Canyon	1000	41
14	*thornei*	North Norton Canyon	60	20
15	*thornei*	South Norton Canyon	500	40
16	*thornei*	Horse Canyon	16	16
17	*thornei*	Box Canyon	150	50
18	*thornei*	Cave Canyon	400	39
19	*thornei*	Eagle Canyon	150	39
20	*thornei*	Eagle-Bryce Canyon	7	7
21	*thornei*	Bryce Canyon	200	39
22	*thornei*	Malo	300	40
23	*thornei*	Canchalagua Canyon	3000	40
24	*kinkiense*	Guds	75	40
Mainland				
1	*variegatum*	Edgewood County Park	200	40
2	*variegatum*	China Camp State Park	100	38
3	*variegatum*	Green Springs Road	40	31
4	*variegatum*	Chinese Station	200	43
5	*variegatum*	Route 49	150	40
6	*variegatum*	Nacimiento-Ferguson Road	200	34
7	*variegatum*	G14	250	40

quent erosion, and loss of shrub and tree cover. In addition, military activities have increased the frequency of fires. The recent elimination of goats has permitted vegetative recovery on the island (Kellogg and Kellogg, 1994).

Seven populations of *D. v. variegatum* were sampled across its range, from Marin County in the north to southern Monterey County and east to Tuolumne and Mariposa Counties. Two of the locations were collected from county parks, two from Fort Hunter Liggett Military Reservation, and three from near roadside habitat. There is no known history of disturbances at any of these locations.

All populations of the three subspecies occurred in open grassland habitat. Island populations were found only on west or northerly aspects, probably due to moister, cooler conditions in these areas.

Tissue collection—Thirty-eight to 50 individuals were haphazardly sampled from large populations (Table 1). In smaller populations, all individuals with many large leaves were sampled. Leaves collected in the field were stored in plastic bags, individually numbered, and kept moist and cool until they were transported to the laboratory, where they were stored at 5°C.

Electrophoresis—Electrophoretic methods followed Soltis et al. (1983). Leaf tissue was crushed in phosphate extraction buffer (Conkle et al., 1982) and stored at −80°C until electrophoresis was conducted.

Three buffer systems were used to resolve loci coding for 14 enzymes. Aspartate aminotransferase (*Aat*), esterase (*Est-1*), malic enzyme (*Me*), phosphoglucomutase (*Pgm*), superoxide dismutase (*Sod*), and triosephosphate isomerase (*Tpi*) were resolved using a lithium hydroxide, pH 8.3 buffer system (Soltis et al., 1983) with 11% starch gels. Diaphorase (*Dia*), florescent esterase (*Est-2*), glyceraldehyde-3-phosphate dehydrogenase (*G3p*), and 6-phosphogluconate dehydrogenase (*Pgd*) were resolved using a tris-borate-EDTA, pH 8.6 buffer system (Soltis et al., 1983) with 11% starch gels. Alkaline phosphatase (*Alp*), malate dehydrodenase (*Mdh*), phosphoglucose isomerase (*Pgi*), and shikimic acid dehydrogenase (*Skd*) were resolved using a tris-citrate, pH 6.3/6.7 buffer system (Selander et al., 1971) with 11.5% starch gels.

Staining recipes for all enzymes followed Soltis et al. (1983), except for *Dia, Sod,* and *Alp* (Murphy et al., 1990). Loci were numbered sequentially, with the most anodally migrating enzyme designated "1." Alleles at a locus were coded alphabetically with the most anodally migrating allozyme designated "a."

Data analysis—Data were analyzed using the computer program Genestrut (Constantine, Hobbs, and Lymbery, 1994). Mean number of alleles per locus (A) and per polymorphic locus (A_P), percentage of polymorphic loci (p), observed heterozygosity (H_O), and expected heterozygosity (H_E) were calculated. Loci were considered polymorphic if more than one allele was detected. Levels of genetic variation were calculated for individual populations and were averaged across all populations on San Clemente Island and all populations of the mainland for geographic comparison. To test for significant differences among these population parameters, t tests were performed after testing for homogeneity of variance. Subspecies-level statistics were calculated by treating all individuals of a subspecies as one population, but the insular subspecies were pooled and comparisons were made between the mainland and the island. Correlations between the measures of genetic variability (A, A_P, p, H_O, and H_E) and estimates of population size were tested using Pearson's correlation analysis (SYSTAT, 1992). Fixation indices (F), reflecting deviations from Hardy-Weinberg equilibrium, were calculated and outcrossing rates (t) were estimated using $t = (1 - F)/(1 + F)$ (Weir, 1990).

The partitioning of genetic diversity within and among all populations was analyzed using F statistics (Nei, 1973). Nei's (1978) unbiased genetic identity (I) was calculated for pairwise comparisons of populations using Genestrut (Constantine, Hobbs, and Lymbery, 1994). The relationship between genetic and geographic distance on San Clemente Island was tested using Mantel (1967) analysis. A cluster analysis was performed using UPGMA (unweighted pair group method with arithmetic mean) and Rogers' (1972) genetic distance.

Gene flow was estimated using Wright's (1951) formula $Nm = (1 - F_{ST})/4F_{ST}$, with F_{ST} considered equivalent to G_{ST} (Nei, 1977). A second estimate was based on the frequency of private alleles (alleles found in a single population; Slatkin, 1985).

RESULTS

Loci and alleles scored—Enzyme electrophoresis resulted in clear and consistent staining for 13 enzymes encoded by 19 putative loci: *Aat, Alp, Dia-1, Dia-2, Est-1, Est-2* (fluorescent), *G3p, Mdh, Me, Pgd-1, Pgd-2, Pgi, Pgm-1, Pgm-2, Skd-1, Skd-2, Sod-1, Sod-2,* and *Tpi*. All enzymes migrated anodally.

Dia-2, G3p, Me, Skd-1, Skd-2, Sod-1, and *Sod-2* were monomorphic, with all individuals from all populations (island and mainland) possessing a single enzyme band with identical mobility for each locus. *Aat, Alp, Est-2, Pgd-1,* and *Pgd-2* were monomorphic for San Clemente Island subspecies. *Pgm-1* was not detected in any of the mainland populations. All other loci were polymorphic in at least one population. In total, the insular subspecies had seven polymorphic loci while the mainland subspecies had 11 polymorphic loci.

Totaled across all 19 loci scored for the island and 18 loci for the mainland, 33 alleles were detected in the two insular subspecies and 47 alleles in the single mainland subspecies. For 11 of 18 loci scored, the most common allele was the same in island and mainland subspecies. At three additional loci, the most common allele was the same in island and mainland subspecies except in the Edgewood Park population. The

TABLE 2. Genetic variability at 19 loci in 31 populations of *Delphinium variegatum*.

Population	A	A_P	p	H_O	H_E	Mean F	t
Delphinium variegatum subsp. *kinkiense* and subsp. *thornei*							
Flasher Canyon	1.26	2.25	21.0	0.084	0.081	−0.032	1.07
Nots Drive	1.26	2.00	26.3	0.063	0.062	−0.019	1.04
Pelican Canyon	1.21	2.00	21.0	0.066	0.072	0.085	0.84
Larkspur Canyon	1.32	2.20	26.3	0.067	0.068	0.015	0.97
Stone Canyon	1.37	2.40	26.3	0.083	0.090	0.081	0.85
Burns-Horton Canyon	1.32	2.20	26.3	0.073	0.081	0.109	0.80
Lower Twin Dams Canyon	1.17	2.00	16.7	0.061	0.075	0.200	0.67
Boulder	1.32	2.00	31.6	0.061	0.081	0.250	0.60
Upper Twin Dams Canyon	1.26	2.00	26.3	0.074	0.071	−0.041	1.09
Warren Canyon	1.28	2.25	22.2	0.071	0.078	0.101	0.82
Upper Middle Ranch Canyon	1.26	2.25	21.0	0.051	0.063	0.187	0.68
Lower Middle Ranch Canyon	1.21	2.00	21.0	0.067	0.085	0.221	0.64
Waynuk Canyon	1.32	2.00	31.6	0.058	0.070	0.171	0.71
North Norton Canyon	1.26	2.25	21.0	0.095	0.084	−0.130	1.30
South Norton Canyon	1.32	2.20	26.3	0.070	0.068	−0.042	1.09
Horse Canyon	1.21	2.00	21.0	0.066	0.075	0.125	0.78
Box Canyon	1.32	2.00	31.6	0.077	0.084	0.087	0.84
Cave Canyon	1.26	2.00	26.3	0.084	0.076	−0.098	1.22
Eagle Canyon	1.37	2.17	31.6	0.085	0.089	0.055	0.90
Eagle-Bryce Canyon	1.21	2.33	15.8	0.038	0.047	0.221	0.64
Bryce Canyon	1.35	2.25	23.5	0.092	0.088	−0.042	1.09
Malo	1.32	2.20	26.3	0.073	0.067	−0.087	1.19
Canchalagua Canyon	1.32	2.50	21.0	0.053	0.063	0.166	0.72
Guds	1.32	2.20	26.3	0.059	0.060	0.021	0.96
Mean	1.28	2.15	24.5	0.070	0.074	0.067	0.90
SE	0.01	0.03	0.9	0.003	0.002	0.023	0.04
Subspecies	1.74	3.00	36.8	0.071	0.078		
Delphinium variegatum subsp. *variegatum*							
Edgewood Park	1.67	2.33	50.0	0.066	0.085	0.222	0.64
China Camp	1.44	3.33	18.8	0.032	0.048	0.333	0.50
Green Springs Road	1.33	2.50	22.2	0.021	0.040	0.479	0.35
Chinese Station	1.50	2.50	33.3	0.037	0.059	0.376	0.45
Route 49	1.44	2.33	33.3	0.031	0.049	0.376	0.45
Nacimiento-Ferguson Road	1.67	2.71	38.9	0.056	0.082	0.317	0.52
G14	1.61	2.67	38.9	0.043	0.086	0.503	0.33
Mean (all mainland)	1.52	2.61	33.6	0.041	0.064	0.372	0.46
SE	0.05	0.13	4.0	0.006	0.007	0.036	0.04
Subspecies[a]	2.61	3.64	61.1	0.043	0.127		

[a] When Edgewood Park is excluded from the analysis, $A = 2.33$, $A_P = 3.18$, $p = 55.6$, $H_O = 0.039$, and $H_E = 0.070$.

common allele was different in island and mainland subspecies at two loci, and no alleles were shared between island and mainland subspecies at two loci. Twenty-five alleles were found in both island and mainland populations. Eight alleles were restricted to the island; four of these were found in only six populations at frequencies ≤5%, one occurred in most populations at frequencies <33%, and three were the most common allele at that locus. Twenty-two alleles were restricted to the mainland; nine of these were unique to single populations, and two were unique to two geographically close populations. The Edgewood Park population had a different common allele than other mainland populations at six loci and had six unique alleles (two of them the most common allele at that locus in Edgewood Park).

The average frequency of alternative alleles was higher in island populations (0.190, ranging from 0.113 to 0.334) than in mainland populations (0.075, ranging from 0.065 to 0.099; $t = 9.63$, df = 28, $P < 0.0001$).

Measures of genetic variability—Standard measures of genetic variability are reported in Table 2. Populations of the two insular subspecies are treated together because there is little morphological evidence to separate them (Dodd and Helenurm, 2000), and there is little genetic differentiation between them (see below). At the population level, genetic variation in insular subspecies was lower than in the mainland subspecies in mean A (1.28 vs. 1.52; $t = 4.81$, df = 7, $P = 0.002$), A_P (2.15 vs. 2.61; $t = 3.43$, df = 7, $P = 0.011$), and p (24.5 vs. 33.6; $t = 2.22$, df = 7, $P = 0.063$). However, populations of the insular subspecies had similar mean H_E (0.074 vs. 0.064; $t = 1.28$, df = 7, $P = 0.241$) and significantly higher mean H_O (0.070 vs. 0.041; $t = 4.45$, df = 9, $P = 0.002$) than the mainland subspecies.

At the subspecies level, the insular taxa had less total genetic variation than the mainland taxon in A (1.74 vs. 2.61), A_P (3.00 vs. 3.64), p (36.8 vs. 55.6), and H_E (0.078 vs. 0.127). However, insular subspecies were higher in H_O (0.071 vs. 0.043). When Edgewood Park was removed from the analysis, the expected heterozygosity of the mainland subspecies was reduced to 0.070 (Table 2).

No significant correlations were found between genetic diversity parameters and estimated population sizes on San Clemente Island (A: Pearson's $r = 0.029$, $P = 0.892$; A_P: Pearson's $r = 0.176$, $P = 0.411$; p: Pearson's $r = -0.056$, $P = 0.793$; H_O: Pearson's $r = -0.186$, $P = 0.384$; H_E: Pearson's $r = -0.140$, $P = 0.514$).

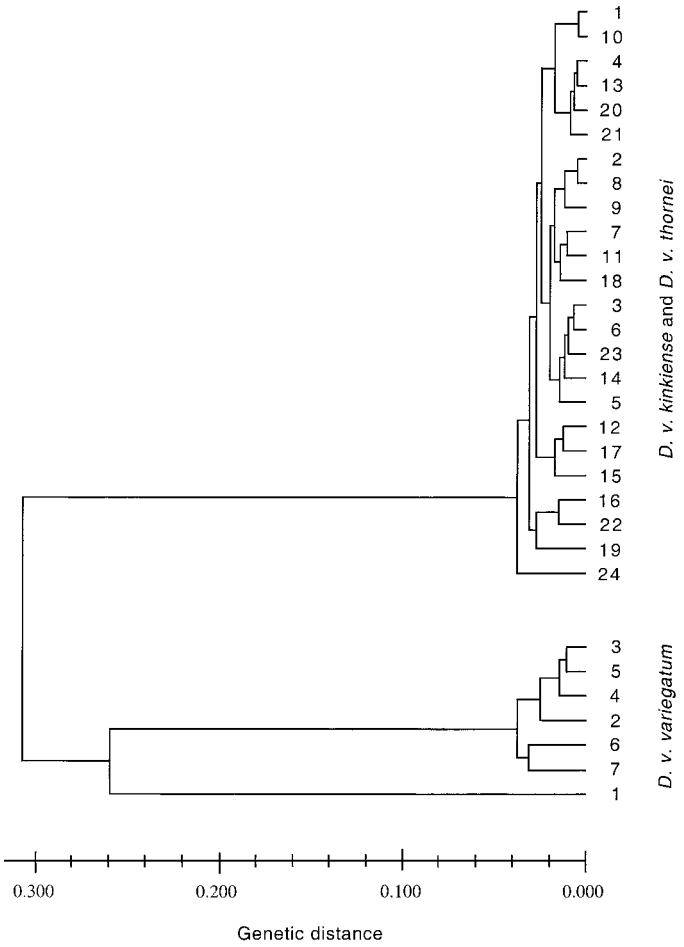

Fig. 2. Cluster analysis of 24 populations of *D. v. kinkiense* and *D. v. thornei* and seven populations of *D. v. variegatum* using unweighted pair group method and Rogers' (1972) genetic distance values.

Genetic identity measures—Genetic identity values (*I*; Nei, 1978) were generally high. Genetic identities for pairs of island populations ranged from 0.976 to 1.000 with a mean of 0.997. Genetic identities for populations of the mainland subspecies ranged from 0.752 to 1.000 with a mean of 0.929. However, if Edgewood Park was excluded, genetic identities for the mainland populations ranged from 0.990 to 1.000 with a mean of 0.996. Genetic identities between island and mainland populations ranged from 0.610 to 0.748 (mean $I = 0.720$) for all populations and from 0.714 to 0.748 (mean $I = 0.734$) excluding Edgewood Park.

The phenogram produced by UPGMA cluster analysis depicts a close genetic relationship among all island populations, with no obvious grouping of populations with respect to taxonomic identity (based on sepal color) or geography (Table 1; Fig. 2). However, a positive relationship exists between genetic and geographic distance for island populations ($t = 4.776$, $P < 0.001$, $N = 24$; Mantel, 1967). Mainland populations showed a similar close grouping, with the exception of Edgewood Park, which appears to be only distantly related to the other *D. v. variegatum* populations. Closer genetic relationships occur among mainland populations in the same geographic area (e.g., populations 3 to 5, and populations 6 and 7).

TABLE 3. Summary of *F* statistics at polymorphic loci of *Delphinium variegatum*. Asterisks indicate F_{ST} values significantly different from zero (*$P < 0.05$, **$P < 0.01$). Values for *Est-1* are not included for *D. v. variegatum* because this locus could not be scored for China Camp State Park.

Locus	F_{IS}	F_{IT}	F_{ST}
D. v. kinkiense and *D. v. thornei*			
Dia-1	−0.008	0.023	0.031**
Est-1	0.226	0.124	−0.004
Mdh	0.742	0.748	0.023*
Pgi	0.072	0.125	0.056*
Pgm-1	0.005	0.000	−0.004
Pgm-2	0.013	0.035	0.022**
Tpi	−0.010	0.026	0.035*
Mean	0.047	0.082	0.037*
D. v. variegatum			
Aat	1.000	1.000	0.178**
Alp	−0.015	0.931	0.932**
Dia-1	0.072	0.093	0.022**
Est-2	0.667	0.986	0.957**
Mdh	−0.024	0.075	0.097**
Pgd-1	1.000	1.000	0.092**
Pgd-2	1.000	1.000	−0.003
Pgi	0.322	0.660	0.498**
Pgm-2	0.100	0.516	0.462**
Tpi	−0.004	−0.009	−0.005
Mean	0.303	0.682	0.543**

Fixation indices and outcrossing rates—Mean fixation indices (*F*) for island populations ranged from −0.130 to 0.250 with mean $F = 0.067$ ($N = 24$), indicating an overall conformance of genotype frequencies to Hardy-Weinberg expectations (Table 2). Twenty-two of 111 fixation indices for individual loci (19.8%) were significant; 18 of these were positive. Mean fixation indices for mainland populations ranged from 0.222 to 0.503 with mean $F = 0.372$, indicating an overall deficiency of heterozygotes. Seventeen of 42 fixation indices for individual loci (42.9%) for mainland populations were significant; all but one were positive.

Outcrossing rates (*t*) based on fixation indices ranged from 0.60 to 1.30 for San Clemente Island populations (mean $t = 0.90$; Table 2), indicating near random mating ($t = 1$ for random mating). In contrast, outcrossing rates for mainland populations ranged from 0.33 to 0.64 (mean $t = 0.46$), indicating considerably higher levels of inbreeding.

F statistics—Mean F_{IS}, representing average deviation from Hardy-Weinberg expectations within populations is low for San Clemente Island populations (mean $F_{IS} = 0.047$; Table 3). Differentiation of populations is low, although significantly different from 0 (mean $F_{ST} = 0.037$, $P < 0.01$). Of the total gene diversity found on San Clemente Island, 97.0% is found within populations and 3.0% is found among populations (mean $H_S = 0.250$, mean $D_{ST} = 0.008$, mean $H_T = 0.257$, $G_{ST} = 0.030$).

Mean F_{IS} and F_{ST} are substantially higher for mainland populations (mean $F_{IS} = 0.303$, $P < 0.01$; mean $F_{ST} = 0.543$, $P < 0.01$), indicating deficiency of heterozygotes compared to Hardy-Weinberg expectations and great differentiation among populations. Removing Edgewood Park from the analysis sharply reduces the measure of differentiation among populations (mean $F_{IS} = 0.316$, $P < 0.01$; mean $F_{ST} = 0.073$, $P < 0.01$). Of the total gene diversity found on the mainland,

45.7% is found within populations and 54.3% is found among populations (mean $H_S = 0.072$, mean $D_{ST} = 0.086$, mean $H_T = 0.158$, $G_{ST} = 0.543$). If Edgewood Park is removed from the analysis, 92.7% of the total genetic diversity is found within populations and only 7.3% is found among populations (mean $H_S = 0.069$, mean $D_{ST} = 0.005$, mean $H_T = 0.074$, $G_{ST} = 0.073$).

Gene flow—Gene flow among San Clemente Island populations was $Nm = 29.9$ using Slatkin's (1985) method based on two private alleles, each with a frequency of 0.013. Wright's (1951) method yielded an estimate of $Nm = 8.1$. Gene flow among the mainland populations was estimated excluding Edgewood Park because of its dissimilarity to other populations of *D. v. variegatum*. Gene flow among the remaining six mainland populations was $Nm = 3.24$ using Slatkin's (1985) method based on eight private alleles with an average frequency of 0.039 (range = 0.013–0.105). Wright's (1951) method gave an estimate of $Nm = 3.2$.

DISCUSSION

Genetic variation and geographic range—The differences in genetic variation between the insular taxa and the mainland subspecies conform to the main predicted differences between narrowly distributed and wide-ranging taxa. The insular endemic taxa *D. v. kinkiense* and *D. v. thornei* have fewer polymorphic loci and fewer alleles per locus than the widespread *D. v. variegatum* at both the population and subspecies levels. This agrees with empirical observations of many plant species (Hamrick and Godt, 1989; Premoli, 1997; Gitzendanner and Soltis, 2000).

However, the endemic insular subspecies have higher levels of observed heterozygosity than their widespread mainland relative at both the population and subspecies levels. The difference in observed heterozygosities appears to be primarily due to differences in the breeding system of the taxa. Fixation indices and outcrossing rates derived from them indicate that the insular subspecies are largely outcrossing, while the mainland subspecies is more highly selfing (in contrast to the common pattern of higher levels of selfing in insular taxa; Barrett, 1996). Differences in breeding system are likely to mainly affect observed heterozygosities rather than other measures of genetic variation because the primary effect of breeding system is to determine the frequencies of diploid genotypes rather than the underlying allele frequencies.

The hypothesis that a breeding system difference affects levels of genetic diversity in *D. variegatum* is also consistent with estimates of gene flow. *Nm* was calculated to be higher for the insular subspecies by both methods of estimation we employed; although both methods may be inaccurate in their estimation of absolute values of gene flow because of assumptions underlying the mathematical models or limitations of data collection (Slatkin, 1994; Whitlock and McCauley, 1999), their congruence in a comparative context is highly suggestive. Gene flow is expected to be higher in outcrossing organisms because self-fertilization precludes the incorporation of genes from other populations. However, the difference in estimates of gene flow may also be partly an artifact of our sampling. We sampled populations throughout the range of the mainland subspecies, resulting in interpopulation distances greater than those for the insular subspecies (although locality records and personal observations suggest that populations of the mainland subspecies are far from each other and may therefore experience less gene flow than island populations).

Expected heterozygosities for populations of the insular endemic subspecies are similar to those of the mainland subspecies in spite of fewer polymorphic loci and alleles per locus. This results from the higher frequencies of alternative alleles at polymorphic loci of island populations, which may be due to the history of disturbance on San Clemente Island. Recent grazing pressure on San Clemente Island by introduced livestock decimated populations of *D. v. kinkiense* and *D. v. thornei* during the last century (Kellogg and Kellogg, 1994). Small populations are vulnerable to genetic drift and especially to the rapid loss of rare alleles. Thus, rare alleles may have been lost on San Clemente Island during the last century, while more common alternative alleles may have persisted through this temporary reduction in population size. It is unclear, however, why the mainland subspecies would be lacking more common alternative alleles.

Some evidence of the action of genetic drift is provided by the UPGMA phenogram (Fig. 2). Even though there is a significant relationship between geographic and genetic distance, suggesting a (metaphorical) island model of isolation-by-distance, there are pairs of populations with high genetic identities that are not geographic neighbors. Moreover, several of the island populations with very few individuals (Lower Twin Dams, Horse, and North Norton Canyons) are not grouped with their nearest geographic neighbor. This may be partly due to the effects of genetic drift on small populations (although sampling error may also be involved: even though all aboveground individuals were sampled in these populations, no dormant seeds were included in the study). It is difficult to know whether current population sizes are correlated with past population sizes because of a lack of quantitative historical data on population sizes and because herbaceous perennials, including *Delphinium* species, may persist belowground without vegetative growth aboveground every year (Epling and Lewis, 1952; Tamm, 1972a, b). There is no overall relationship between population size in 1996 and genetic diversity parameters.

Expected heterozygosity is higher for the widespread mainland subpecies at the subspecies level only due to the Edgewood Park population, which is highly differentiated from the other mainland populations. If this population is not included, expected heterozygosities are similar due to higher alternative allele frequencies at polymorphic loci of the insular subspecies.

Thus, we propose that the observed patterns of genetic diversity in *D. variegatum* are caused mainly by geographic range and breeding system, with an additional contribution from the genetic drift caused by recent disturbance leading to small population sizes on San Clemente Island. This is consistent with Hamrick and Godt's (1989) conclusion that geographic range and breeding system are the major characteristics affecting levels of genetic diversity in populations.

Genetic divergence—If the Edgewood Park population of *D. v. variegatum* is excluded from analyses, the island and mainland taxa of *D. variegatum* partition their variation similarly. The mean genetic identities between island populations and between mainland populations are high, and G_{ST} values for the island and mainland taxa are similar (0.030 and 0.073, respectively) and very low compared with the average $G_{ST} = 0.224$ for plants (Hamrick and Godt, 1989). The similar par-

TABLE 4. Genetic variability measures in *Delphinium variegatum* compared with published levels of genetic variation in two congeners and in other plant species based on geographic distribution. Standard errors are provided in parentheses.

Taxon or Category	A		*p*		H_E	
	Populations	Taxon	Populations	Taxon	Populations	Taxon
Delphinium variegatum subsp. *kinkiense* and subsp. *thornei*						
Mean	1.28 (0.01)	1.74	24.53 (0.91)	36.8	0.074 (0.002)	0.078
Range	1.17–1.37	—	15.79–31.58	—	0.047–0.090	—
Delphinium variegatum subsp. *variegatum*						
Mean	1.52 (0.05)	2.61	33.63 (4.01)	55.6	0.064 (0.007)	0.127
Range	1.44–1.67	—	18.75–50.00	—	0.040–0.086	—
Delphinium viridescens[a]						
Mean	1.6	2.50	35.3	70.0	0.119	0.149
Range	1.3–2.0	—	20.0–60.0	—	0.048–0.159	—
Delphinium bolosii[b]						
Mean	1.63	1.75	50.0[e]	58.3	0.117	0.129
Range	1.58–1.67	—	50.0–50.0	—	0.109–0.125	—
Allozyme diversity review[c]						
Endemic	1.39 (0.03)	1.80 (0.08)	26.3 (2.1)	40.0 (3.2)	0.063 (0.006)	0.096 (0.010)
Narrow	1.45 (0.05)	1.83 (0.08)	30.6 (2.2)	45.1 (2.8)	0.105 (0.009)	0.137 (0.011)
Regional	1.55 (0.04)	1.94 (0.06)	36.4 (2.0)	52.9 (2.1)	0.118 (0.007)	0.150 (0.008)
Widespread	1.72 (0.07)	2.29 (0.16)	43.0 (3.3)	58.9 (3.1)	0.159 (0.013)	0.202 (0.015)
Congeneric comparisons[d]						
Rare	1.53 (0.10)	1.94 (0.21)	29.9 (3.8)	36.7 (4.9)		0.219 (0.022)
Widespread	1.66 (0.09)	2.23 (0.25)	36.3 (3.6)	44.9 (4.9)		0.242 (0.028)

[a] Richter et al., 1994.
[b] Bosch et al., 1998.
[c] Hamrick and Godt, 1989.
[d] Gitzendanner and Soltis, 2000.
[e] Using <1.00 criterion.

titioning of genetic variation in subspecies of *D. variegatum* is consistent with the observation that geographic range is not significantly associated with G_{ST} values (Hamrick and Godt, 1989). If Edgewood Park is included in analyses, the mainland subspecies shows substantial genetic differentiation among populations ($G_{ST} = 0.543$) compared to the endemic subspecies. However, this population is morphologically as well as genetically differentiated from other populations of *D. v. variegatum* (see below; Dodd and Helenurm, 2000), and its inclusion in a comparison of genetic variation may be inappropriate.

The UPGMA phenogram groups pairs of populations of *D. v. variegatum* that are geographically close, suggesting that levels of gene flow are higher for adjacent than for widespread populations. No clear geographic grouping occurs for populations of the insular endemic subspecies.

Comparison with other species—*Delphinium variegatum* appears to be fairly typical of plant species in its levels of genetic variation relative to geographic range at both the population and taxon levels (Table 4). The San Clemente Island subspecies, *D. v. kinkiense* and *D. v. thornei*, exhibit levels of genetic variability very close to the average for endemic species for all measures of genetic variation. The mainland subspecies *D. v. variegatum* has levels of genetic variation relatively close to the average for regional species for most measures of genetic variation but is higher than average in A_P at the taxon level (due to Edgewood Park) and lower than expected in H_E at both the population and species levels (due to the low average frequencies of alternative alleles).

Levels of genetic diversity in *D. v. kinkiense* and *D. v. thornei* also appear to be somewhat typical of insular endemic plant taxa. DeJoode and Wendel (1992) reviewed data from 69 insular endemic plants in 16 genera with lower average species-level values of genetic diversity ($p = 0.25$, $A = 1.32$, $H_T = 0.064$). Frankham (1997) reviewed comparisons of closely related insular endemic and mainland plant taxa and found that in nine of ten cases the insular endemic species is less heterozygous than its mainland congener. Genetic diversity in the insular endemic subspecies of *D. variegatum* ($H_T = 0.257$) is considerably higher than in endemic plants of the Canary Islands ($H_T = 0.186$ for 69 species in 18 genera) and other island archipelagos ($H_T = 0.064$; Francisco-Ortega et al., 2000).

The genetic variation we observed appears to be low for the genus *Delphinium*. Genetic studies have been reported of two other endemic species in this genus with highly restricted distributions. *Delphinium viridescens* is known from only 17 populations in an area 30 km long and 10 km wide in central Washington, USA (Richter, Soltis, and Soltis, 1994), and *D. bolosii* is known from only two populations within 100 km of each other in Catalonia, Spain (Bosch et al., 1998). Populations of these narrowly distributed species have more polymorphic loci, more alleles per locus, and higher heterozygosities than the insular endemic subspecies of *D. variegatum* (Table 4); their levels of genetic diversity are consistent with what is usually observed for regionally distributed species.

Genetic differentiation among populations appears to be generally low in the genus *Delphinium*. *F* statistics indicate substantial differentiation among populations of *D. viridescens* ($F_{ST} = 0.209$), but this is due primarily to 1 or 2 of 17 populations, with most populations being genetically very similar

(Richter, Soltis, and Soltis, 1994). Differentiation is low among six populations of *D. nuttallianum* (Williams and Waser, 1999).

Taxonomy—Our results do not provide clear genetic evidence to separate *D. v. kinkiense* and *D. v. thornei*, the two insular subspecies. Most alleles are shared among all populations with differences detected primarily in allele frequencies. F_{ST} and G_{ST} values indicate very little genetic differentiation among the set of San Clemente Island populations, and the mean genetic identity between island populations is very high. The UPGMA phenogram groups populations of the insular taxa without regard to taxonomic identity. Moreover, gene flow among the 24 island populations appears to be high enough to prevent differentiation, if our estimates of historical gene flow are any indication of current gene flow. However, populations that are geographically close have higher genetic identities than populations separated by greater distance, suggesting higher levels of gene flow among adjacent populations.

These findings parallel results from a study of floral variation in populations of *D. variegatum*, in which sepal color was shown to be the only known character that differentiates the insular subspecies (Dodd and Helenurm, 2000). Both morphological and genetic data thus indicate that populations of *D. variegatum* on San Clemente Island are very similar. Further taxonomic study is recommended to determine whether the insular taxa have been correctly designated as separate subspecies. The two insular taxa may be better classified as varieties rather than subspecies or classified together as one subspecies (as defined by Stuessy, 1990). However, other characters may clearly separate these taxa and should be investigated. Reclassification may have implications for legal protection of these taxa, as only *D. v. kinkiense* is federally listed as endangered. Even if *D. v. kinkiense* and *D. v. thornei* are combined, they are still rare and therefore at risk of extinction due to their very localized distribution.

In contrast to the homogeneity of island populations of *D. variegatum*, populations of the mainland subspecies *D. v. variegatum* are genetically heterogeneous. Edgewood Park is genetically very distinct from other mainland populations, with lower genetic identity values and more unique alleles than other populations. It is also differentiated morphologically from other populations of *D. v. variegatum* in that it has larger flowers (Dodd and Helenurm, 2000). Thus, *D. v. variegatum* may consist of two separate lineages. Subsequent to sampling, we discovered that Edgewood Park is the only population we sampled that occurs on serpentine soils. Warnock (1990b) considers serpentine soil populations of *D. v. variegatum* to be not well marked morphologically and did not recognize them as a distinct taxon. Instead, Warnock (1997) comments that plants with large flowers are common in the San Francisco Bay area, either as scattered individuals or as populations made up largely of such individuals.

In other species, plants growing on serpentine soils have often been documented to be morphologically distinct from plants growing on nonserpentine soils (Kruckeberg, 1954; Mayer, Soltis, and Soltis, 1994), but serpentine soil populations have not generally been found to differ at allozyme loci from nonserpentine populations. In *Streptanthus glandulosus* subsp. *glandulosus*, genetic identity is high for populations in close proximity regardless of soil type, and there are no clusters of serpentine and nonserpentine populations (Mayer, Soltis, and Soltis, 1994). However, certain populations exhibit distinctive allozymic and morphological profiles that may be caused by genetic drift in small, isolated populations with low levels of gene flow (Mayer, Soltis, and Soltis, 1994). Sampling of additional natural populations of *D. v. variegatum* may clarify whether serpentine soil populations are differentiated genetically (at allozyme loci) and morphologically from nonserpentine populations or whether the variation is geographic in pattern.

Implications for conservation—The federally endangered *D. v. kinkiense* and its rarer relative *D. v. thornei* are both endemic to San Clemente Island. Together they are known only from 24 populations distributed throughout the island (although additional scattered individuals are occasionally observed) ranging in size from 16 to several thousand individuals (Fig. 1; Table 1). Thus, these taxa have a narrow range, few populations, and often small populations. In spite of this rarity, *D. variegatum* on San Clemente Island is not markedly genetically depauperate; the levels of genetic variation we observed are typical of endemic species (although low for the genus, since other narrowly endemic *Delphinium* species have more polymorphic loci and alleles; Table 4; Richter, Soltis, and Soltis, 1994; Bosch et al., 1998). The long-term prospects for *D. v. kinkiense* and *D. v. thornei* may be favorable if populations are allowed to recover and expand even further. Genetic drift should not rapidly erode genetic diversity as long as military activities do not reduce or further restrict populations. Additional favorable genetic diversity may even arise through mutation if population sizes continue to increase.

Populations of *D. variegatum* on San Clemente Island appear to be almost equivalent genetically, regardless of taxonomic designation or geographic location. This is convenient for protection of an endangered taxon in a military area in which training activities regularly occur. The genetic data suggest that choice of training area can be relatively independent of genetic considerations, because the loss of any single population is unlikely to cause a significant loss of genetic variation for the taxon. However, the high degree of similarity among populations and the positive relationship between genetic and geographic distance is likely to be due to gene flow. Thus, an important management guideline is to prevent the isolation of populations (or groups of populations) through extirpation of intervening populations. Isolation would restrict gene flow and permit both the loss of genetic variation (possibly even favorable alleles; Hartl, 1988) within populations and the consequent differentiation among populations through genetic drift. If populations are lost due to military activities, then remaining populations should be prioritized according to both genetic and geographic criteria: populations containing different allele frequencies and less common alleles or whose locations minimize distances for gene flow should be provided extra protection.

The observed pattern of genetic variation also has implications for reintroduction and ex situ conservation. The high genetic identities and estimates of *Nm* suggest that enough gene flow occurs to prevent significant differentiation of populations. Thus, the possibility of local adaptation of populations is less likely than for many other taxa. Reintroductions using seeds from any convenient seed source may be feasible; careful choice of a seed source to match the reintroduction site by proximity, soil type, or associated vegetation may not be necessary. Moreover, mixing of seeds from different sources appears unlikely to jeopardize reintroduction efforts. Finally,

the allozyme data suggest that ex situ collections, especially desirable as a safeguard against extirpation of populations of narrowly distributed taxa with a small number of populations (Lande, 1988; Simberloff, 1988), may not need to include seeds from each population.

LITERATURE CITED

BABBEL, G. R., AND R. K. SELANDER. 1974. Genetic variability in edaphically restricted and widespread plant species. *Evolution* 28: 619–30.

BARRETT, S. C. H. 1996. The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London Series B* 351: 725–733.

BARRETT, S. C. H., AND J. R. KOHN. 1991. Genetic and evolutionary consequences of small population size. *In* D. A. Falk and K. E. Holsinger [eds.], Genetics and conservation of rare species, 3–30. Oxford University Press, New York, New York, USA.

BASKAUF, C. J., D. E. MCCAULEY, AND W. G. EICKMEIER. 1994. Genetic analysis of a rare and a widepread species of *Echinacea* (Asteraceae). *Evolution* 48: 180–188.

BOSCH, M., J. SIMON, J. MOLERA, AND C. BLANCHE. 1998. Reproductive biology, genetic variation and conservation of the rare endemic dysploid *Delphinium bolosii* (Ranunculaceae). *Biological Conservation* 86: 57–66.

COLE, C. T., AND D. B. BIESBOER. 1992. Monomorphism, reduced gene flow, and cleistogamy in rare and common species of *Lespedeza* (Fabaceae). *American Journal of Botany* 79: 567–575.

CONKLE, M. P., P. HODGSKISS, L. NUNNALLY, AND S. HUNTER. 1982. Starch gel electrophoresis of conifer seeds: a laboratory manual. General Technical Report PSW-64. USFS, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

CONSTANTINE, C. C., R. P. HOBBS, AND A. J. LYMBERY. 1994. FORTRAN programs for analyzing population structure from multilocus genotypic data. *Journal of Heredity* 85: 336–337.

CRAWFORD, D. J., T. F. STUESSY, D. W. HAINES, M. B. COSNER, M. SILVA O., AND P. LOPEZ. 1992. Allozyme diversity within and divergence among four species of *Robinsonia* (Asteraceae: Senecioneae), a genus endemic to the Juan Fernandez Islands, Chile. *American Journal of Botany* 79: 962–966.

DEJOODE, D. R., AND J. F. WENDEL. 1992. Genetic diversity and origin of the Hawaiian Islands cotton, *Gossypium tomentosum*. *American Journal of Botany* 79: 1311–1319.

DODD, S. C., AND K. HELENURM. 2000. Floral variation in *Delphinium variegatum* (Ranunculaceae). *Madrono* 47: 116–126.

ELLSTRAND, N. C., AND D. R. ELAM. 1993. Population genetic consequences of small populations size: implications for plant conservation. *Annual Review of Ecology and Systematics* 23: 237–261.

EPLING, C., AND H. LEWIS. 1952. Increase of the adaptive range of the genus *Delphinium*. *Evolution* 6: 253–267.

FRANCISCO-ORTEGA, J., A. SANTOS-GUERRA, S. C. KIM, AND D. J. CRAWFORD. 2000. Plant genetic diversity in the Canary Islands: a conservation perpective. *American Journal of Botany* 87: 909–919.

FRANKHAM, R. 1997. Do island populations have less genetic variation than mainland populations? *Heredity* 78: 311–327.

FRANKLIN, I. R. 1980. Evolutionary change in small populations. *In* M. E. Soule and B. A. Wilcox [eds.], Conservation biology: an evolutionary-ecological perspective, 135–149. Sinauer, Sunderland, Massachusetts, USA.

GITZENDANNER, M. A., AND P. S. SOLTIS. 2000. Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany* 87: 783–792.

HAMRICK, J. L., AND M. J. W. GODT. 1989. Allozyme diversity in plant species. *In* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir [eds.], Plant population genetics, breeding and genetic resources, 43–63. Sinauer, Sunderland, Massachusetts, USA.

HARTL, D. L. 1988. A primer of population genetics, 2nd ed. Sinauer, Sunderland, Massachusetts, USA.

HOLSINGER, K. E., AND L. D. GOTTLIEB. 1991. Conservation of rare and endangered plants: principles and prospects. *In* D. A. Falk and K. E. Holsinger [eds.], Genetics and conservation of rare plants, 195–208. Oxford University Press, New York, New York, USA.

JUNAK, S. A., AND D. H. WILKEN. 1998. Sensitive plant status survey, Naval Auxiliary Landing Field, San Clemente Island, California. Santa Barbara Botanic Garden Technical Report No. 1, Santa Barbara, California, USA.

KADEREIT, J. W., H. P. COMES, D. J. CURNOW, J. A. IRWIN, AND R. J. ABBOTT. 1995. Choroplast DNA and isozyme analysis of the progenitor-derivative species relationship between *Senecio nebrodensis* and *S. viscousus* (Asteraceae). *American Journal of Botany* 82: 1179–1185.

KARRON, J. D. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* 1: 47–58.

KELLOGG, E. M., AND J. L. KELLOGG. 1994. San Clemente Island vegetation condition and trend and the elements of ecological restoration. Prepared for Southwest Division Naval Facilities Engineering Command, San Diego. Tierra Data Systems, Reedley, California, USA.

KRUCKEBERG, A. R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* 35: 267–274.

KRUCKEBERG, A. R., AND D. RABINOWITZ. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16: 447–479.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455–1460.

LEWIS, H., AND C. EPLING. 1954. A taxonomic study of Californian *Delphiniums*. *Brittonia* 8: 1–22.

LINHART, Y. B., AND A. C. PREMOLI. 1993. Genetic variation in *Aletes acaulis* and its relative, the narrow endemic *A. humulis* (Apiaceae). *American Journal of Botany* 80: 598–605.

MANTEL, N. 1967. The detection of disease and a generalized regression approach. *Cancer Research* 27: 209–220.

MAYER, M. S., P. S. SOLTIS, AND D. E. SOLTIS. 1994. The evolution of the *Streptanthus glandulosus* complex (Cruciferae): genetic divergence and gene flow in serpentine endemics. *American Journal of Botany* 81: 1288–1299.

MUNZ, P. A. 1969. California miscellany VII. *Aliso* 7: 65–71.

MURPHY, R. W., J. W. SITES, D. B. BUTH, AND G. H. HAUFLER. 1990. Proteins 1: isozyme electrophoresis. *In* D. M. Hillis and C. Moritz [eds.], Molecular systematics, 45–127. Sinauer, Sunderland, Massachusetts, USA.

NEI, M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences, USA* 70: 3321–3323.

NEI, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics* 41: 225–233.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.

NEI, M., T. MARUYAMA, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10.

NICKRENT, D. L., AND D. WIENS. 1989. Genetic diversity in the rare California shrub *Dedeckera eurekensis* (Polygonaceae). *Systematic Botany* 14: 245–253.

PLEASANTS, J. M., AND J. F. WENDEL. 1989. Genetic diversity in a clonal narrow endemic, *Erythronium propullens*, and its progenitor, *Erythronium albidum*. *American Journal of Botany* 76: 1136–1151.

PREMOLI, A. C. 1997. Genetic variation in a geographically restricted and two widespread species of South American *Nothofagus*. *Journal of Biogeography* 24: 883–892.

RABINOWITZ, D. 1981. Seven forms of rarity. *In* H. Synge [ed.], The biological aspects of rare plant conservation, 205–217. Wiley, New York, New York, USA.

RAVEN, P. H. 1963. A flora of San Clemente Island, California. *Aliso* 5: 289–347.

RAVEN, P. H., AND D. I. AXELROD. 1978. Origin and relationships of the California flora. University California Press, Berkeley, California, USA.

RICHTER, T. S., P. S. SOLTIS, AND D. E. SOLTIS. 1994. Genetic variation within and among populations of the narrow endemic, *Delphinium viridescens* (Ranunculaceae). *American Journal of Botany* 81: 1070–1076.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics VII. *University of Texas Publication* 7213: 145–153.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in genetics VI. *University of Texas Publication* 7103: 49–90.

SIMBERLOFF, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Sytematics* 19: 473–511.

SKINNER, M. W., AND B. M. PAVLIK. 1994. California Native Plant Society

inventory of rare and endangered vascular plants of California. California Native Plant Society, Sacramento, California, USA.

SLATKIN, M. 1985. Rare alleles as indicators of gene flow. *Evolution* 39: 53–65.

SLATKIN, M. 1994. Gene flow and population structure. *In* L. A. Real [ed.], Ecological genetics, 3–17. Princeton University Press, Princeton, New Jersey, USA.

SOLTIS, D. E., C. H. HAUFLER, D. C. DARROW, AND G. H. GASTONY. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *American Fern Journal* 73: 9–27.

STUESSY, T. F. 1990. Plant taxonomy: the systematic evaluation of comparative data. Columbia University Press, New York, New York, USA.

SYSTAT. 1992. SYSTAT: statistics, version 5.2 ed. SYSTAT, Evanston, Illinois, USA.

TAMM, C. O. 1972a. Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. *Oikos* 23: 23–28.

TAMM, C. O. 1972b. Survival and flowering of perennial herbs. III. The behaviour of *Primula veris* on permanent plots. *Oikos* 23: 159–166.

VAN VALEN, L. 1965. Morphological variation and width of ecological niche. *American Naturalist* 99: 377–390.

WARNOCK, M. J. 1990a. New taxa and combinations in North American *Delphinium* (Ranunculaceae). *Phytologia* 68: 1–6.

WARNOCK, M. J. 1990b. Taxonomic and ecological review of California *Delphinium*. *Collectanea Botanica* 19: 45–74.

WARNOCK, M. J. 1993. *Delphinium*. *In* J. C. Hickman [ed.], The Jepson manual: higher plants of California, 916–922. University of California Press, Berkeley, California, USA.

WARNOCK, M. J. 1997. *Delphinium*. *In* Flora of North America Editorial Committee [ed.], Flora of North America, vol. 3, 196–240. Oxford University Press, New York, New York, USA.

WEIR, B. S. 1990. Genetic data analysis. Sinauer, Sunderland, Massachusetts, USA.

WHITLOCK, M. C., AND D. E. MCCAULEY. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity* 82: 117–125.

WILLIAMS, C. F., AND N. M. WASER. 1999. Spatial genetic structure of *Delphinium nuttallianum* populations: inferences about gene flow. *Heredity* 83: 541–550.

WRIGHT, S. 1931. Evolution in Mendelian populations. *Genetics* 28: 114–138.

WRIGHT, S. 1951. The genetic structure of populations. *Annals of Eugenics* 15: 323–354.