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GENETIC VARIATION IN ENDEMIC AND WIDESPREAD PLANT SPECIES: EXAMPLES FROM SAXIFRAGACEAE AND *POLYSTICHUM* (DRYOPTERIDACEAE)[1]

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ABSTRACT

Population genetic theory and methodology were applied to the study of endemic plant species. Levels of genetic variability were compared between endemic species and their more widespread relatives. Six of seven narrowly distributed taxa of Saxifragaceae had significantly reduced genetic diversity relative to species of Saxifragaceae with broader distributions. Two endemic species of the fern *Polystichum* maintained significantly lower levels of genetic variation than did their more widespread congeners. The implications of these data and those reported for other endemic plant species for designing management strategies are also discussed.

Key words: endemic plant species, allozymic variation, Saxifragaceae, *Polystichum*.

INTRODUCTION

A recent resurgence of interest among biologists of many disciplines in the conservation and preservation of endangered species has led to the incorporation of population genetic theory and methodology into the study of endemic species of both plants and animals. Population genetic theory predicts that endemic species will maintain low levels of genetic variation, and this prediction is borne out in many endemics, particularly island endemics (e.g., Lowrey and Crawford 1985; Crawford, Stuessy, and Silva 1987; Witter and Carr 1988). These low levels of genetic variation are probably due to the small numbers of individuals present within each population and also the small number of individuals in the species as a whole. Small population sizes typically result in the loss of genetic variation through genetic drift. Furthermore, small populations result in an increased probability of mating between relatives, causing inbreeding even in cross-pollinated plants. Highly inbred populations are also susceptible to loss of genetic variation. Endemic plant species may also have reduced genetic variation for other reasons. 1) The species may have experienced a severe genetic bottleneck, through which only a small proportion of the genetic variation passed. Bottlenecks of this sort may occur when most populations of a species are eliminated, either gradually or catastrophically. 2) The endemic species may represent a recently derived species. In many cases, recent derivatives have only a fraction of the genetic variation of their more widespread progenitors (Gottlieb 1974; Crawford and Smith 1982).

Despite this theoretical interest in levels of genetic variation in endemic plant species, actual measurements of genetic variation in endemics have only been made in recent years. The value of assessing genetic variability in endemic plant species is at least three-fold:

1) The amount of genetic variation in a population or species is a key to

unraveling the evolutionary history of that population or species. Although "low" levels of genetic variation are predicted for all endemic plant species, the actual genetic diversity may be useful in evaluating alternative evolutionary hypotheses.

2) Levels of genetic variation are often equated with evolutionary potential. If a species is totally lacking in genetic variability, it may have difficulty adapting to changing environmental conditions.

3) Genetic variability in endemic species of both plants and animals has become increasingly important to managers of rare and endangered species. The levels and distribution of genetic variation within and among populations of an endemic species may suggest to conservationists how many populations to preserve and which ones contain different genotypes.

Electrophoretic techniques provide the best estimate of genetic variation in natural populations, and allozymic analyses of endemic species have become much more frequent in the last few years. Several statistics can be used to quantify levels of genetic variation within a population: P, the percentage of loci that are polymorphic within a population; H, heterozygosity expected at Hardy-Weinberg equilibrium; H_{obs}, the observed heterozygosity; A, the mean number of alleles per locus; and A_p, the mean number of alleles per polymorphic locus. These values are computed for each population sample of a species; then a mean value for each statistic can be determined for the species.

Levels of genetic variation in a population or species can be affected by several factors, such as the geographic distribution of the species, the generation time, pollination syndrome, fecundity, and successional stage of the habitat (Hamrick, Linhart, and Mitton 1979). Generally, a species from a late successional stage, with a regional distribution, a long generation time, wind pollination, and high fecundity can be expected to maintain high levels of genetic variation within its populations.

Hamrick (1983) summarized levels of genetic variation in populations of species having different geographical distributions: his categories were endemic, narrow, regional, and widespread. The statistics of genetic variation used were H and A_p. These data showed that high levels of genetic variation are maintained in many populations of endemic plant species. In fact, in direct contrast to all predictions, endemic species are nearly as variable as widespread species. It therefore appears that although some endemics, particularly those from islands, have the low levels of genetic variation predicted, others maintain quite high levels of genetic variation.

A comparison such as Hamrick's (1983) survey is rather coarse grained: the geographic categories are somewhat arbitrary and unrelated species with totally different life histories are compared. To resolve these problems, Karron (1987) compared levels of genetic variation in species with restricted distributions with genetic variability in their more widespread congeners. He defined a restricted species as an "extremely localized endemic that occurs in 20 or fewer populations; in many cases, taxa have fewer than 20,000 individuals." Karron examined species in 11 genera and compared them for P and A_p. A statistical analysis indicated that both P and A_p are significantly lower in the restricted species than in their widespread congeners. That is, when congeneric species are compared, populations of the endemics maintain lower levels of genetic variation than do populations of their more widespread relatives, exactly as population genetic theory predicts.

The discrepancy between these results and those of Hamrick (1983) is probably due to the comparison of unrelated taxa in the earlier study.

These broad surveys of genetic variation in endemic plants suggest that although genetic variation is lower in restricted species than in their widespread congeners, many endemic plant species maintain relatively high levels of genetic variation. In fact, Hamrick concluded his 1983 study with this statement:

> . . . although the results indicated that more populations of narrow and regionally distributed species will be needed to maintain a given proportion of the species' variation, recommendations based on geographic range alone will not be dependable.

GENETIC VARIATION IN ENDEMIC SPECIES: EXAMPLES

Saxifragaceae

Levels of genetic variation in the endemic species *Conimitella williamsii, Bensoniella oregona, Elmera racemosa, Sullivantia hapemanii, S. oregana,* and *S. sullivantii* were compared with genetic variability in more widespread members of Saxifragaceae, including six species of *Heuchera* and the monotypic *Tellima* and *Tolmiea. Conimitella, Bensoniella,* and *Elmera* are monotypic and belong to a group of nine closely related genera in tribe Saxifrageae (Soltis 1988). *Sullivantia* is part of a second group of Saxifrageae consisting of four genera (Soltis 1988). All are herbaceous perennials, all are diploid with a chromosome number of $n = 7$, and most occur in western North America.

Conimitella williamsii has a broad geographic distribution (Hitchcock, Cronquist, Ownbey, and Thompson 1961) but it occupies a narrow ecological niche. The species occurs in the Rocky Mountains from southwestern Montana through eastern Idaho into western Wyoming, in the Bighorn Mountains of eastern Wyoming, and in Colorado. Despite this relatively large distribution, it occurs only rarely on wooded slopes. Chloroplast DNA data indicate that *C. williamsii* is the sister species of *Mitella stauropetala* Piper (Soltis, Soltis, and Bothel 1990). We analyzed genetic variation at 18 loci in two populations of *C. williamsii* from western Wyoming and one from Colorado. No variation was detected in the smaller sample from Wyoming or in the sample from Colorado; only one locus was polymorphic in the large population from Wyoming. Very little genetic variation is maintained within populations of *C. williamsii. P* and *A* are 0.037 and 1.1, respectively (Table 1). The mean value of *P* for the widespread Saxifragaceae is much higher (0.216), although *A* is similar (1.2; Table 1). Despite this lack of variation within populations, variation was detected among populations. Populations from Wyoming and Colorado are fixed for different alleles at *Pgi-2* and *Skdh,* the genes encoding cytosolic phosphoglucoisomerase and shikimate dehydrogenase, respectively. Although the species has not been sampled from other parts of its range, such as Montana or northeastern Wyoming, the data currently available suggest that there may be considerable variation among populations of this species.

The levels and distribution of genetic variation in *C. williamsii* may be related to several factors. 1) A phylogenetic analysis of *Mitella* and its relatives using cpDNA data indicates that *C. williamsii* must be relatively recent in origin because it occupies a terminal position on the evolutionary tree (D. Soltis et al. 1990).

However, its wide distribution indicates that it cannot be too recent in origin. 2) Populations are physically isolated and probably do not experience much interpopulational gene flow. Both seed and pollen flow appear limited (Savile 1975), and the allozymic data support this contention. 3) Plants are predominantly selfing; all individuals set seed in the greenhouse in the absence of pollinators. All of these factors may contribute to the low levels of genetic variation within populations and the differentiation among populations of *C. williamsii.*

Bensoniella oregona has a very restricted distribution, occurring only in mesic drainages in the Siskiyou Mountains of southwestern Oregon and northwestern California. Chloroplast DNA data indicate that *B. oregona* is closely related to *Mitella* and is probably a relictual lineage that diverged from *Mitella* early in the radiation of *Mitella* (D. Soltis et al. 1990). We analyzed genetic variation at 21 loci in samples from four sites in southwestern Oregon. No genetic variation was detected, either within or among populations.

The low genetic variability of *B. oregona* may reflect the relictual nature of this species. The cpDNA data clearly suggest that *B. oregona* is a very old lineage. Its distribution also suggests that it may be a relict; the Siskiyou area is known to harbor many relictual species (Smith and Sawyer 1988). If *B. oregona* is indeed a relict, it has apparently experienced a severe genetic bottleneck that has culled additional genetic variation. In addition to its narrow distribution, several life-history characteristics of *B. oregona* might also lead to reduced genetic variability: small population sizes, isolated populations, clonal reproduction (each "site" may actually be a single genetic individual), and a high degree of self-pollination.

Elmera racemosa occurs on talus slopes at high elevations in the Pacific Northwest. Variety *racemosa* is found in the Olympic Mts. and in the Cascades from Mt. Rainier to Mt. Adams; var. *puberulenta* Hitchc. occurs in the Cascades from northern Washington to the vicinity of Mt. Stuart in central Washington and also disjunctly in northwestern Klamath County, Oregon. The phylogenetic affinities of *E. racemosa* are uncertain although it is morphologically intermediate between *Tellima* and species of *Heuchera.* Karyotypic analysis of the three genera indicated that all were distinct; however, the karyotype of *E. racemosa* is more similar to that of *Heuchera* than to that of *Tellima.* A single population of *E. racemosa* var. *puberulenta* from just south of Mt. Stuart has been examined allozymically at 12 loci. This population was highly variable genetically (Table 1). Both *P* and *A* for this population (0.333 and 1.3, respectively) were higher than the means of these statistics for the widespread species of Saxifragaceae. This genetic variability was unexpected because *E. racemosa* shares many features with *C. williamsii* and *B. oregona* which may contribute to the low levels of genetic variation in these other two species, including a limited distribution and small, isolated populations. The age and phylogenetic position of the *Elmera* lineage are unknown; these may provide a clue to the high levels of genetic variation in *E. racemosa.*

All three species of *Sullivantia* (*sensu* Soltis 1980) were also examined. Species of *Sullivantia* occur on wet cliffs, often associated with waterfalls. *Sullivantia sullivantii* is relatively widespread in eastern North America, occurring in three major regions: the Ohio River Valley of Indiana and Ohio; the Mississippi River Valley of Iowa, Wisconsin, and Illinois; and the Ozarks. *Sullivantia hapemanii* var. *hapemanii* occurs in the Bighorn Mountains of northeastern Wyoming, and var. *purpusii* occurs in western Colorado. *Sullivantia oregana* occurs in the Co-

Table 1. Mean values of P and A for species of Saxifragaceae with restricted and widespread distributions. The number of populations of each species examined is given in parentheses.

Species	P	A	Reference
Restricted species			
Conimitella williamsii (Eaton) Rydb. (3)	0.037	1.1	unpubl. data*
Bensoniella oregona (Abrams & Bacig.) Morton (4)	0.000	1.0	unpubl. data*
Elmera racemosa (Wats.) Rydb. (1)	0.333	1.3	unpubl. data*
Sullivantia hapemanii (Coulter & Fisher) Coulter			
var. *hapemanii* (5)	0.033	1.0	Soltis (1982)
var. *purpusii* (Brand.) Soltis (3)	0.000	1.0	Soltis (1982)
S. oregana Wats. (3)	0.000	1.0	Soltis (1982)
S. sullivantii (T. & G.) Britton (18)	0.000	1.0	Soltis (1982)
Mean	0.058	1.1	
Widespread species			
Heuchera americana L. (12)	0.21	1.1	Soltis (1985)
H. parviflora Barthing (4)	0.29	1.2	Soltis (1985)
H. pubescens Pursh (4)	0.14	1.1	Soltis (1985)
H. villosa Michx. (4)	0.29	1.3	Soltis (1985)
H. grossulariifolia Rydb.† (14)	0.238	1.4	Wolf, Soltis, and Soltis (1990)
H. micrantha Dougl.† (9)	0.241	1.4	Ness, Soltis, and Soltis (1989)
Tellima grandiflora (Pursh) Dougl. (9)	0.080	1.1	Rieseberg and Soltis (1987)
Tolmiea menziesii (Pursh) T. & G.† (15)	0.240	1.3	Soltis and Soltis (1989)
Mean	0.216	1.2	

* Collection data and loci examined for populations of these species are summarized in Appendix I. A table of allele frequencies for populations of species for which data have not been previously published is available upon request from the authors.

† Data presented are for the diploid ($2n = 14$) cytotype only.

lumbia River Gorge of Washington and Oregon. Statistics of genetic variation for the four taxa of *Sullivantia* are shown in Table 1. Despite its relatively broad distribution, populations of *S. sullivantii* have no genetic variation. However, populations are fixed for different alleles at *Acp,* the gene encoding acid phosphatase (Soltis 1982). The three more restricted taxa also have little or no genetic variation, either within or among populations. The only taxon with any intrapopulational variation is *S. hapemanii* var. *hapemanii,* which has two populations polymorphic for two alleles at *Acp.* Founder events, genetic bottlenecks, and genetic drift have probably all been important in reducing genetic variation in both restricted and more widespread species of *Sullivantia* (Soltis 1982).

Several endemic species of Saxifragaceae maintain low levels of genetic variability, and a single population of another species possesses an unexpected amount of genetic variation. How do these levels of genetic variation compare with levels for more widespread members of Saxifragaceae? All of the eight species with broader distributions have higher levels of genetic variation than do *C. williamsii, B. oregona,* and all species of *Sullivantia*; however, the mean values for all eight widespread species are lower than those for the single population of *E. racemosa* from Mt. Stuart. Mean values of P and A for both the endemic and widespread species of Saxifragaceae are given in Table 1. Using the Wilcoxon two-sample test, both measures of genetic variation are statistically significantly lower ($P <$

0.05) in the endemics than in the widespread species. This agrees with Karron's (1987) results for restricted and widespread congeners in 11 genera.

Polystichum

Genetic variation in two endemic species of North American *Polystichum, P. dudleyi* and *P. lemmonii,* was analyzed relative to that maintained by their more widespread congeners. An analysis of allozymic variation in diploid North American polystichums indicates that the strictly North American species form a group distinct from the circumboreal *P. lonchitis* (L.) Roth (Soltis, Soltis, and Wolf 1990). Within this group of five species, the western North American *P. dudleyi* and *P. lemmonii,* along with the eastern North American *P. acrostichoides,* form one group, and *P. munitum* and *P. imbricans* from western North America form a second group.

Polystichum dudleyi is restricted to canyons of redwood forest in the Coast Ranges of central California, from southern Mendocino County to Monterey County, where it typically occupies steep slopes above streams. We analyzed genetic variation at 12 loci in 11 populations of *P. dudleyi,* and the data are summarized in Table 2. Mean levels of genetic variation for all the populations are low; most of the populations had only a single polymorphic locus. The values for *P. dudleyi* are much lower than the means for the more widespread species of *Polystichum* (Table 2).

Polystichum dudleyi has a narrow distribution. Its habitat is certainly restricted, and it probably occupies relictual sites. Populations of *P. dudleyi* maintain very low levels of genetic variation, possibly due to a genetic bottleneck. Furthermore, populations are physically isolated from each other in canyons. Despite high outcrossing rates and high levels of interpopulational gene flow (Soltis and Soltis 1990), *P. dudleyi* is genetically depauperate.

Polystichum lemmonii is a serpentine endemic, occurring in central Washington, central and southwestern Oregon, and northern California. We analyzed genetic variation at 12 loci in six populations of *P. lemmonii,* two populations from Washington, one from southwestern Oregon, and three from California. The genetic variability of *P. lemmonii* is summarized in Table 2. Populations of *P. lemmonii* maintain higher levels of genetic variation than do populations of *P. dudleyi,* but lower levels than those typically seen in more widespread polystichums.

The three main geographic areas occupied by *P. lemmonii* are well separated spatially. Populations are isolated on serpentine soils at high elevations; this isolation may contribute to their relatively low levels of genetic variation. Furthermore, the adaptation of *P. lemmonii* to serpentine soils may be reflected in a highly specialized genotype, with limited variability.

When compared with their closest relative, *P. acrostichoides,* both *P. dudleyi* and *P. lemmonii* have low levels of genetic variation (Table 2). The other two strictly North American species also have high levels of genetic variation (Table 2). Values of P and A for the endemics are lower ($P < 0.10$) than those for the widespread species. However, using the Wilcoxon two-sample test, the values for the endemics are not statistically significantly lower presumably because this nonparametric test is conservative, especially when sample sizes are small.

Table 2. Mean values of *P* and *A* for species of *Polystichum* with restricted and widespread distributions. The number of populations of each species examined is given in parentheses.

Species	*P*	*A*	Reference
Restricted Species			
Polystichum dudleyi Maxon (11)	0.083	1.1	P. Soltis et al. (1990)
P. lemmonii L. Underwood. (6)	0.250	1.3	P. Soltis et al. (1990)
Mean	0.166	1.2	
Widespread Species			
P. acrostichoides (Michaux) Schott (7)	0.444	1.6	P. Soltis et al. (1990)
P. imbricans (D. Eaton) D. Wagner (12)	0.500	1.8	P. Soltis et al. (1990)
P. munitum (Kaulf.) K. Presl (25)	0.394	1.6	P. Soltis et al. (1990)
Mean	0.446	1.7	

DISCUSSION

In general, endemic plant species maintain lower levels of genetic variation than do their widespread relatives. However, exceptional endemics, such as *E. racemosa* and others, actually maintain high levels of genetic variation. These data reinforce the observation that geographic distribution alone is not a reliable indicator of genetic variability. What implications do these data have for the conservation and management of rare and endangered plant species? The first general principle followed by conservation geneticists is to maintain or preserve as much genetic variation as possible. Hamrick (1983) determined that 99% of a species' genetic diversity is maintained within a single population of an outcrossing species. He therefore recommends that at least four populations of an endangered outcrossing species be preserved. Because inbreeders typically distribute relatively more of their genetic variation among rather than within populations, Hamrick recommends that at least six populations of an endangered inbreeding species be preserved. Furthermore, to preserve genetic diversity via seed stocks for potential reintroduction, A. H. D. Brown (pers. comm.) recommends preserving seed from 10–50 individuals per population and at least five populations per species. The second general principle is to consider factors other than allozymic variability when designing a management strategy. Genetic data should never be the sole criterion for management decisions. For example, parameters such as the mating system, morphological diversity, life history, and local adaptation should also be considered.

The importance of preserving several populations of an endangered species cannot be overemphasized, even in cases where no genetic variation was detected via allozymic analyses. Genetic variation for other biochemical characters or morphological characters may exist. Saving several populations increases the probability that additional genetic variation will be preserved. Furthermore, if only one or two populations are preserved, the species is in danger of extinction due to catastrophic events such as floods or fires. The preservation of additional populations reduces this risk. Finally, each endemic species is distinct in its genetic attributes. There are no unfailing generalizations; therefore each endemic species of interest should be examined for its genetic properties and the factors that affect them before management decisions are made.

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FOOTNOTE

[1] Based on a lecture presented by Pamela S. Soltis at the Fifth Annual Southwestern Botanical Systematics and Evolution Symposium, *Endemism,* 19–20 May 1989, Rancho Santa Ana Botanic Garden, Claremont, California 91711.

Appendix I. Collection data, enzymes examined, and loci interpreted for populations of *Conimitella williamsii, Bensoniella oregona,* and *Elmera racemosa.* Electrophoretic procedures followed Soltis, Haufler, Darrow, and Gastony (1983).

Conimitella williamsii

Collection data:
Colorado. Summit Co.:
Ute Pass, along stream flowing into Blue River, *Soltis 1508.*
Wyoming. Sublette Co.:
Hoback River, 5.4 mi N of Bondurant, *Soltis 1500.*
Hoback River, 5.9 mi N of Bondurant, *Soltis 1496.*

Enzymes examined:
Aldolase (ALD), Catalase (CAT), Fluorescent Esterase (FE), Leucine Aminopeptidase (LAP), Malate Dehydrogenase (MDH), Phosphoglucoisomerase (PGI), Phosphoglucomutase (PGM), Shikimate Dehydrogenase (SkDH), Triosephosphate Isomerase (TPI)

Loci interpreted:
Ald, Cat, Fe-1, Fe-2, Fe-3, Lap-1, Lap-2, Mdh-1, Mdh-2, Mdh-3, Mdh-4, Pgi-1, Pgi-2, Pgm-1, Pgm-2, Skdh, Tpi-1, Tpi-2

Bensoniella oregona

Collection data:
Oregon. Josephine Co.:
Bear Camp Pasture, *Lang, Soltis, & Soltis s.n.*
USFS Rd. 2309, 1 mi from USFS Rd. 23, *Lang, Soltis, & Soltis s.n.*
USFS Rd. 2309, 0.25 mi from USFS Rd. 23, *Lang, Soltis, & Soltis s.n.*
Meadow off of USFS Rd. 2308, *Lang, Soltis, & Soltis s.n.*

Enzymes examined:
Catalase (CAT), Fluorescent Esterase (FE), Glyceraldehyde 3-phosphate Dehydrogenase ([NAD]G3PDH), Isocitrate Dehydrogenase (IDH), Leucine Aminopeptidase (LAP), Malate Dehydrogenase (MDH), Phosphoglucoisomerase (PGI), Phosphoglucomutase (PGM), Shikimate Dehydrogenase (SkDH), Superoxide Dismutase (SOD), Triosephosphate Isomerase (TPI)

Loci interpreted:
Cat, Fe-1, Fe-2, Fe-3, G3pdh, Idh, Lap, Mdh-1, Mdh-2, Mdh-3, Mdh-4, Pgi-1, Pgi-2, Pgm-1, Pgm-2, Skdh-1, Skdh-2, Sod-1, Sod-2, Tpi-1, Tpi-2

Elmera racemosa

Collection data:
Washington. Kittitas Co.:
Headwaters of Beverly Creek, *Soltis & Soltis 2179.*

Enzymes exmained:
Glyceraldehyde 3-phosphate Dehydrogenase ([NAD]G3PDH), Isocitrate Dehydrogenase (IDH), Leucine Aminopeptidase (LAP), Malate Dehydrogenase (MDH), Phosphoglucoisomerase (PGI), Phosphoglucomutase (PGM), Shikimate Dehydrogenase (SkDH), Triosephosphate Isomerase (TPI)

Loci interpreted:
G3pdh, Idh, Lap, Mdh-1, Mdh-2, Mdh-3, Pgi-1, Pgi-2, Pgm-1, Pgm-2, Skdh, Tpi