

2001

Comparative genetics of seven plants endemic to Florida's Lake Wales Ridge

Eric S. Menges

Rebecca W. Dolan

Butler University, rdolan@butler.edu

Rebecca Yahr

Doria R. Gordan

Follow this and additional works at: http://digitalcommons.butler.edu/facsch_papers



Part of the [Forest Sciences Commons](#), and the [Plant Sciences Commons](#)

Recommended Citation

Menges, E.S., Dolan, R.W., Yahr, R. & Gordon, D.R. (2001). Comparative genetics of seven plants endemic to Florida's Lake Wales Ridge. *Castanea*, 66 (1-2), pp. 98-114. Available from: http://digitalcommons.butler.edu/facsch_papers/138.

This Article is brought to you for free and open access by the College of Liberal Arts & Sciences at Digital Commons @ Butler University. It has been accepted for inclusion in Scholarship and Professional Work - LAS by an authorized administrator of Digital Commons @ Butler University. For more information, please contact fgaede@butler.edu.

Comparative Genetics of Seven Plants Endemic to Florida's Lake Wales Ridge

ERIC S. MENGES,¹ REBECCA W. DOLAN,² REBECCA YAHR,³ and DORIA R. GORDON⁴

¹Archbold Biological Station, PO Box 2057, Lake Placid, Florida 33862;

²Friesner Herbarium, Butler University, Indianapolis, Indiana 46208;

³Department of Botany, Box 90338, Duke University, Durham, North Carolina 27708;

⁴The Nature Conservancy, Department of Botany, University of Florida, Gainesville, Florida 32611

ABSTRACT

Genetic variation is often low in narrowly endemic species, and may be further depleted by habitat loss and fragmentation. Few studies have tested predictions about the distribution of genetic variation among co-occurring endemic plants species. We describe genetic variation and its relationship to life history traits for seven narrowly endemic, federally endangered Florida scrub species: *Dicerandra christmanii*, *D. frutescens*, *Eryngium cuneifolium*, *Hypericum cumulicola*, *Liatris ohlingerae*, *Nolina brittoniana*, *Warea carteri*. These species have varying life histories, degrees of habitat specialization, and geographic distributions. Measures of genetic (allozyme) diversity (mean number of alleles/locus, percentage of loci polymorphic and expected heterozygosity) varied among species. However, genetic variation was generally lower than published means for plants and also generally lower for means for comparable groups (endemics, short-lived herbs, species with mixed mating systems, species with gravity dispersed seeds). The chief exception was *L. ohlingerae*, which had relatively high genetic variation. All three measures of genetic variation produced the same ranking among species: *L. ohlingerae* > *D. christmanii* > *N. brittoniana* > *E. cuneifolium* > *D. frutescens* > *W. carteri* > *H. cumulicola*. For six of these species, we compared genetic variation with rankings of eight life history factors. Genetic variation was highest in long-lived, demographically stable, outcrossing species with long pollinator dispersal distances. Attributes such as median population size, habitat specificity, geographic range, and estimated primary seed dispersal distances were not related to rankings for genetic variation. The studied species varied widely in genetic differentiation among populations ($0.02 < F_{ST} < 0.72$). The most differentiated species, *H. cumulicola*, is pollinated by specialized bees that may move short distances, therefore limiting gene flow among isolated patches. These comparisons emphasize that co-occurring narrowly endemic species can have a diversity of genetic patterns and that many factors can influence the amount and distribution of genetic variation. Further loss of genetic variation due to habitat loss and fragmentation will impact the genetic variation of these species differently. A single conservation strategy for this suite of species is therefore unlikely to achieve genetic conservation goals.

INTRODUCTION

Plant populations are subject to the disruptive effects of systematic influences such as altered disturbance regimes, exotic species encroachment, or successional changes, and to stochastic demographic and environmental factors (Menges 1997). Any or all of these factors may contribute to diminished population sizes. In addition, rare species often naturally exist as small, isolated populations that are susceptible to random genetic forces implicated in the loss of genetic variation over time in small populations (Huenneke 1991, Oostermeijer et al. 1995). The presence of genetic diversity allows plants to adapt to changing conditions or new selection pressures (Barrett and Kohn 1991, Huenneke 1991, Frankel et al. 1995). However, it is unclear what measures of genetic diversity or allele abundance may be most important to prioritize for conservation (Marshall and Brown 1975, Falk 1991). High priority populations may be chosen on the basis of unique alleles (Petit et al. 1998), alleles at self-incompatibility loci (Young et al.

1999), localized common alleles (Brown 1978), overall genetic differences among populations (Kress et al. 1994, Young and Brown 1996), and/or maximizing overall genetic variation (Sun 1996, Ceska et al. 1997).

The collection and analysis of genetic data permit the evaluation of potential and historic gene flow. Gene flow is crucial in controlling population differentiation and genetic variation within individual populations (Wright 1977, Bradshaw 1994). As habitat patches supporting populations become increasingly isolated by habitat fragmentation, gene flow is predicted to decrease. Past levels of gene flow can be inferred from genetic statistics such as F_{ST} (Wright 1951), the proportion of the total variation found among, as opposed to within, populations. F_{ST} is a measure of population differentiation (Wright 1965) that is often correlated with life history strategies.

Population genetic diversity, spatial patterns of genetic variation, and gene flow affect both individual fitness and the scale at which conservation of populations will be effective (Byers 1998). Although narrow endemics tend to have relatively low genetic variation (Hamrick et al. 1991, Gitzendanner and Soltis 2000), they can display a diversity of patterns (e.g., Karron 1991). Few studies have compared patterns of genetic variation in several co-occurring endemic plant species (but see Prober et al. 1990, Lewis and Crawford 1995, Godt et al. 1996, McDonald and Hamrick 1996), and most of these studies are of a single pair of species.

Genetic surveys are often considered as integral elements in modern conservation biology, particularly in planning for effective long-term conservation of species (Schemske et al. 1994). Maintenance of gene flow may influence the location of reserves in a larger system. On the other hand, reserves that are isolated beyond the reach of normal gene flow need to support populations large enough to prevent genetic erosion via drift (Barrett and Kohn 1991).

Genetic surveys of Florida scrub plants have begun recently. A dominant species, sand pine [*Pinus clausa* (Chapm. ex Englem.) Vasey ex Sarg.] had low genetic variation and population differentiation (Parker and Hamrick 1996). In contrast, Lewis and Crawford (1995) found unexpectedly high variation in narrowly distributed scrub *Polygonella* species. The very narrowly endemic shrub *Ziziphus celata* had little genetic variation (Godt et al. 1997). A previous study that considered two of the species of this paper (*Dicerandra frutescens*, *Eryngium cuneifolium*) surveyed only 1–2 populations per endemic species (McDonald and Hamrick 1996), which does not permit much detail on trends within species. This paper is the first to consider more than two Florida scrub species or large numbers of populations per species.

In this paper, we compare the distribution of genetic variation in seven federally endangered plant species of Florida scrub (*Dicerandra christmanii* Huck and Judd, *D. frutescens* Shinners, *Eryngium cuneifolium* Small, *Hypericum cumulicola* (Small) W.P. Adams, *Liatris ohlingerae* (S.F. Blake) B.L. Rob., *Nolina brittoniana* Nash, and *Warea carteri* Small). The species are all narrowly distributed in central Florida, grow in Florida scrub, and presumably have been exposed to similar selection pressures, including xeric soil conditions and infrequent, high-intensity fires (Menges 1999). However, the species have different distributions within their ranges, varied life histories, and different degrees of specialization for habitats and soil types. Allozyme analyses based on extensive field sampling are used to characterize genetic variation in all seven species.

We also evaluate eight factors that may be responsible for genetic differences among species: species range, habitat specificity, longevity, demographic stability, population size, breeding system, pollinator movements, and primary seed dispersal. Genetic variation tends to be relatively high in longer-lived perennials, widespread species, outcrossing species, and well-dispersed plants (Hamrick et al. 1991, Gitzendanner and Soltis 2000). We also predicted that greater gene flow via pollen movement or seed dispersal could maintain species' genetic variation (Barrett and Kohn 1991), that demographically variable species might have lost variation through bottlenecks and drift (Barrett and Kohn 1991), that larger populations might have retained genetic variation (Young et al. 1996), and that habitat-restricted plants might have lower genetic variation (Hamrick and Godt 1989, Gray 1996).

METHODS

Sites, Tissue Collections, and Allozyme Analyses

The seven study species are all largely found on, and four are endemic to, Florida's Lake Wales Ridge (LWR, Figure 1). The LWR is an ancient dune system that supports one of the nation's most imperiled endemic-rich ecosystems (Dobson et al. 1997), including more than 20 species of narrowly endemic vascular plants, 2 endemic vertebrates, and dozens of endemic invertebrates (Christman and Judd 1990, Deyrup and Franz 1994). Most of the endemic species are found in Florida scrub, a naturally-patchy ecosystem dominated by shrubs and characterized by infrequent, intense fires (Menges 1999). The naturally patchy distribution and antiquity of Florida scrub has led to extremely strong geographic patterns in genetic diversity in the Florida scrub lizard (Clark et al. 1999). Less than 15% of the historical area of Florida scrub habitat remains (Peroni and Abrahamson 1985), with remnants scattered as islands within a matrix of agriculture and development. The endemic species have always been patchily distributed and are further threatened by subsequent habitat loss and fragmentation.

We sampled a total of 165 populations from 57 localities across four central Florida counties (Highlands, Lake, Orange, and Polk; Figure 2). These populations spanned three ridges (Lake Wales, Winter Haven, and Orlando, Figure 1). Sites were identified using distributional data from the Florida Natural Areas Inventory (FNAI, Tallahassee, Florida) and our own field surveys, which include several newly discovered populations. Criteria for selecting sampling sites included sampling across entire species' ranges and collecting leaves from populations with at least 10 individuals. Only a few samples (4 of 30 for *Liatris ohlingerae*; 5 of 48 for *Nolina brittoniana*) had fewer than 15 individuals. We selected sites located at least 1.6 km apart, gaining permission from landowners. We sampled most intensively from publicly and privately owned conservation sites or from those sites proposed for conservation acquisition.

We collected tissue for allozyme analyses (flower buds from *Hypericum cumulicola* and leaves from the other six species) from each of the 165 populations. For populations smaller than 30 plants, we collected from each individual. For larger populations, we collected from 30 individuals selected in a stratified random or haphazard fashion from throughout the spatial extent of the population. Leaves were placed in plastic bags and stored on ice in the field and in the refrigerator prior to shipping. Leaves were shipped overnight with wet paper towels to Butler University and again stored cold until allozyme analyses were run. The methods of Dolan (1994, 1995) were followed for allozyme extraction, gel scoring for putative loci and alleles, and calculation of standard genetic statistics (Swofford and Selander 1989). Pairwise genetic similarity between populations was calculated using Nei's unbiased genetic identity (Nei 1978). We re-sampled material from the earliest sampled populations to check for consistency of results over time.

Genetic individuals are readily distinguished for all species in this study, with the exception of *N. brittoniana*, a clonal plant that produces clusters of rosettes. We considered plants of this species separated by at least one meter as separate individuals. This rule is consistent with the grouping of different genders (plants are subdioecious), and allozyme analyses of neighboring plants (data not shown).

Life History Factors

To evaluate hypotheses for species differences in the distribution of genetic variation, we incorporated information from a number of related studies. Population sizes in all collection sites were estimated by direct counts (generally for all populations smaller than 200 plants) or by extrapolation from counts in belt transects (2–4 m wide) to totals for habitat patches. Patches were mapped in the field or mapped using digitized, geo-referenced aerial photographs, with ARC/INFO 3.2 software (ESRI 1996). The boundaries of populations were defined by >50 m gaps between plants or between suitable habitat patches. We used geographic information in digital form from FNAI, along with our own observations, to construct GIS coverages in ARC/INFO and ARCVIEW of species' distributions (known locations) and ranges (suitable and

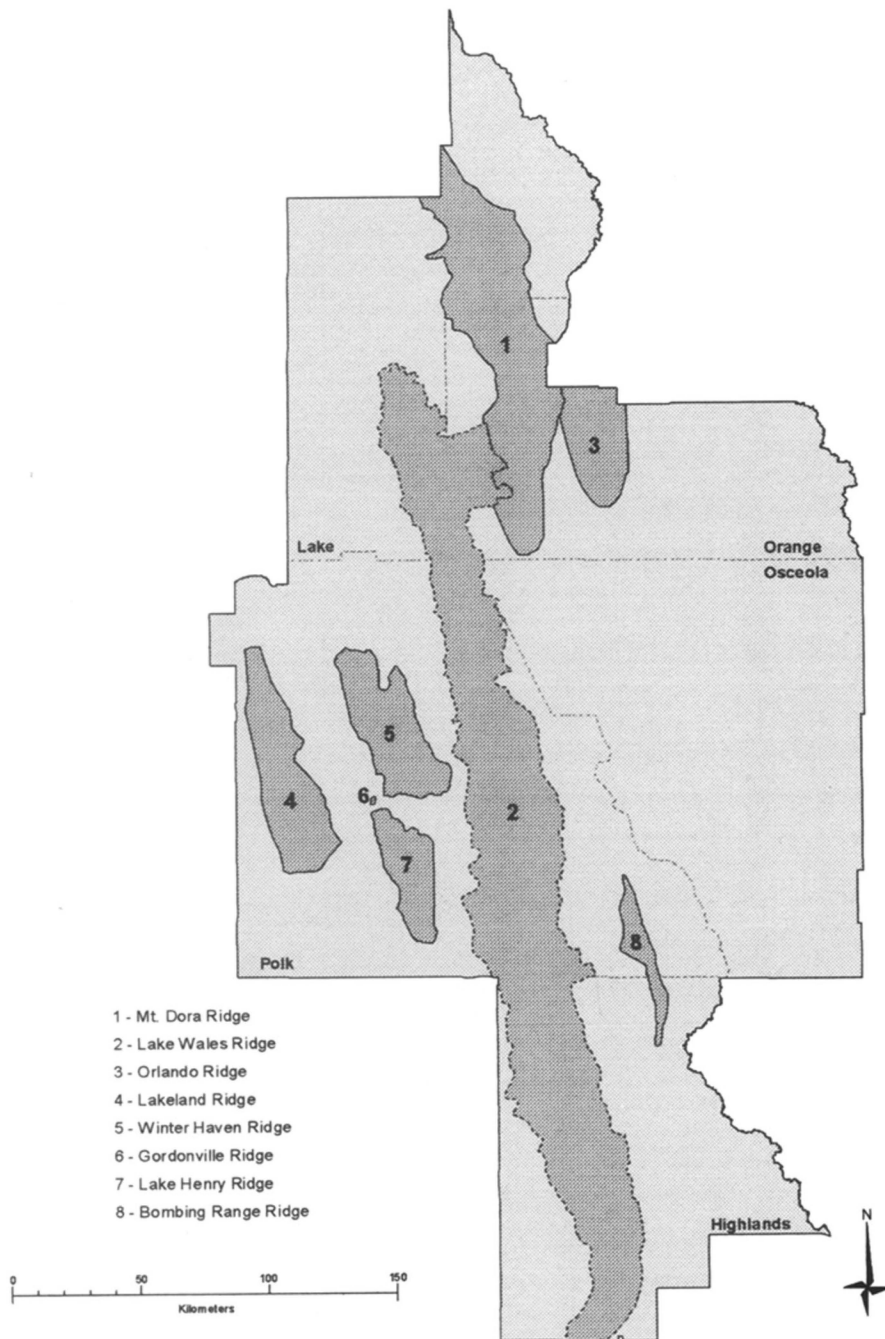


Figure 1. Upland ridges of central Florida. Names and boundaries follows White 1970 and Brooks 1981, as interpreted by Eric Menges, Carl Weekley, and Roberta Pickert for GIS coverages.

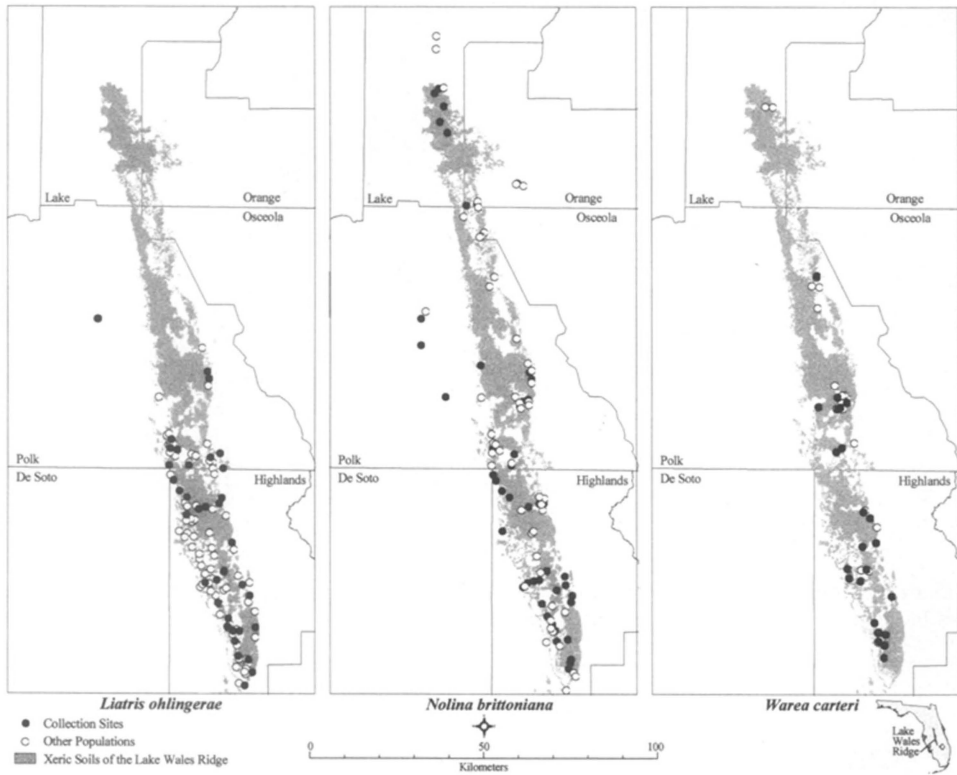
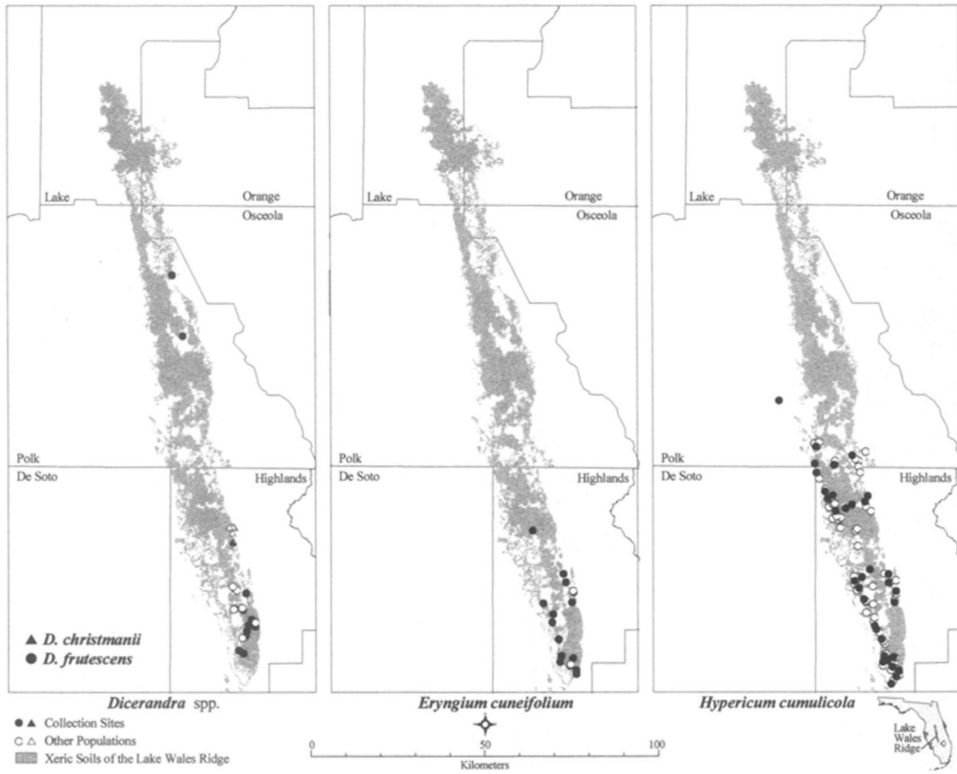


Table 1. Sampling effort and population-level genetic statistics for seven Lake Wales Ridge species, listed from high to low H_e , and summary statistics (below line) from Hamrick and Godt (1989). [Number of species in parentheses, number of populations is a mean value; H_e reported as total genetic diversity ($H_{e, \text{total}} = 1 - \sum p_i^2$, where p_i is the frequency of the i th allele in each population); and G_{ST} is reported instead of F_{ST} ; these are comparable statistics (Swofford and Selander 1989)]

Species or Group	NP	NI	L	A/L	PLP	H_e	F_{ST}	GI
<i>Liatrix ohlingerae</i>	30	22.0	12	1.46	31.4	0.121	0.120	0.987
<i>Dicerandra christmanii</i>	1	30.0	11	1.40	18.2	0.088	NA	NA
<i>Nolina brittoniana</i>	48	25.4	15	1.26	16.0	0.069	0.411	0.949
<i>Eryngium cuneifolium</i>	16	30.0	21	1.19	16.0	0.054	0.445	0.954
<i>Dicerandra frutescens</i>	13	24.5	18	1.18	7.7	0.031	0.030	0.999
<i>Warea carteri</i>	23	25.4	25	1.10	6.8	0.025	0.304	0.989
<i>Hypericum cumulicola</i>	34	28.2	18	1.08	6.2	0.023	0.724	0.937
All Species (473)	13	NA	16.5	1.53	34.2	0.113	0.224	NA
Endemic Species (81)	6	NA	17.8	1.39	26.3	0.063	0.248	NA
Mixed Animal Mating (64)	9	NA	14.4	1.43	29.2	0.090	0.216	NA
Gravity-Dispersed (161)	10	NA	16.9	1.45	29.8	0.101	0.277	NA
Short Lived Perennial Herbs (119)	9	NA	7.1	1.40	28.0	0.096	0.233	NA

NP: Number of populations; NI: Mean number of individuals sampled per population; L: Number of loci; A/L: Mean alleles per locus; PLP: Mean percent loci polymorphic; H_e : Expected heterozygosity; F_{ST} : Proportion of total variation found among populations; GI: Nei's Genetic Identity; NA: Data not available.

potential habitat). Comparisons of known species distributions with soil survey data (Carter et al. 1989, Ford et al. 1990) allowed us to define the habitat and soil preferences of each species.

Life span information was obtained from a series of long-term (up to 11 years) demographic studies of each species. Perennial plants were studied using permanently marked or mapped plants in quadrats or macroplots at Archbold Biological Station, Highlands County, Florida and other sites (Menges 1992, Menges and Kimmich 1996, Menges and Gordon 1996, Quintana-Ascencio and Morales-Hernandez 1997, Thomas et al. 1998, Menges et al. 1999). We annually counted plants of the annual *Warea carteri* in defined areas at many sites (Menges and Gordon 1996). In addition, we studied temporal demographic stability in population size in permanent plots. Responses to fire were examined in many of these studies as well as obtained from a more general survey (Menges and Kohfeldt 1995, Menges and Hawkes 1998). We characterized the breeding systems and pollinator movements for each species based on individual detailed studies of each species (Menges et al. 1998, Evans et al. 2000). Primary seed dispersal inferences were made from laboratory experiments in still air (Menges et al. 1998).

Rankings of species for various genetic measures were made, and compared to rankings based on non-genetic data. We used six species sampled from multiple populations in the ranking analysis, since we were able to sample only one population of *Dicerandra christmanii*. The small number of species precluded the use of rank statistics.

RESULTS

A Comparison of Species: Overall Patterns of Genetic Variation

Results of the allozyme analysis varied widely among species (Table 1). Between 11 and 25 loci were clearly and consistently resolved. Among species, alleles per locus (A/L) ranged

←

Figure 2. Ranges of seven endemic species of Florida scrub plants, showing the Lake Wales Ridge, known occurrences (all circles) and populations sampled (closed circles) for genetic analysis; a) *Dicerandra* spp., *Eryngium cuneifolium*, *Hypericum cumulicola*; b) *Liatrix ohlingerae*, *Nolina brittoniana*, *Warea carteri*.

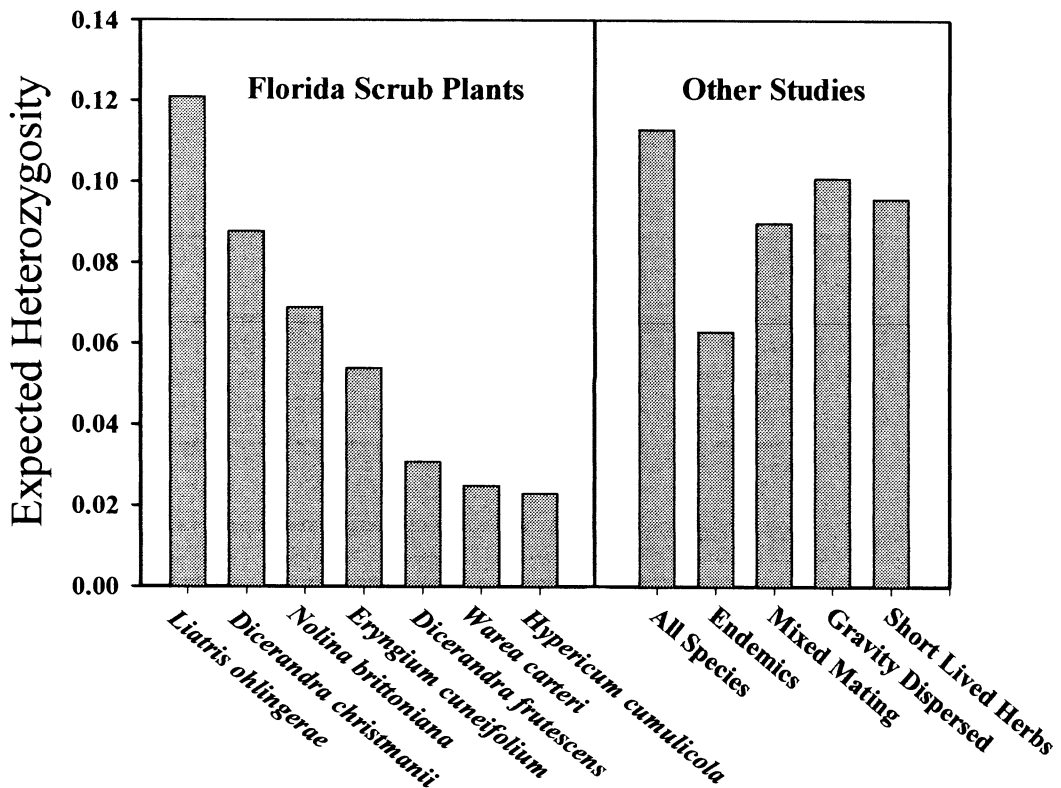


Figure 3. Expected heterozygosity for each of seven Florida scrub endemic plants, in comparison to published means for comparable groups from Hamrick and Godt (1989).

from 1.08–1.46, the percentage of loci polymorphic (PLP) spanned 6–31%, and expected heterozygosity (H_e) varied from 0.023–0.121 (Table 1, Figure 3). Compared to a previously published survey (Hamrick and Godt 1989), 20 of 21 of these population-level genetic statistics for these Florida scrub species (7 species, 3 comparable statistics for each) were lower than means for all plant species (Table 1). The exception was *Liatris ohlingerae*, which had a greater value for H_e (0.121) than the mean for all species (0.113). Florida scrub genetic variation was also generally lower than means for endemic species (15/21 statistics; 3 of the 6 exceptions were *L. ohlingerae* [A/L, PLP, H_e]; also *Dicerandra christmanii* [A/L and H_e], and *Nolina brittoniana* [H_e]; Table 1). Comparisons to species with mixed mating systems, to species with gravity dispersed seeds, and to short-lived herbs (Hamrick and Godt 1989) showed lower values for comparable species of Florida scrub (Table 1). *L. ohlingerae*, with relatively high values, is self-incompatible, with wind dispersal and a long life span.

Among the seven species, rankings based on A/L, PLP, and H_e were identical (Table 1). In order from greatest value to least, the species ranks were, *Liatris ohlingerae* > *Dicerandra christmanii* > *Nolina brittoniana* > *Eryngium cuneifolium* > *D. frutescens* > *Warea carteri* > *Hypericum cumulicola* (Figure 3).

The distribution of genetic variation among populations varied widely among species. Values for F_{ST} showed that 3–72% of species' genetic variation were found among populations (Table 1). *Hypericum cumulicola* had notably higher differentiation among populations ($F_{ST} = 0.72$) than any of the other species ($0.03 < F_{ST} < 0.45$). Two of the six species (*L. ohlingerae*, *D. frutescens*) had F_{ST} values below the published means for all species, endemics, species with mixed-mating systems, gravity-dispersed species, or short-lived herbs. Nei's genetic identities

Table 2. Population size, range information, habitats, and soils occupied by each Florida scrub endemic species in the study

Sp*	Medi-an Pop Size	Counties** (no. of pops)	Ridges‡ (no. of pops)	Habitats‡‡	Soils***
<i>Lo</i>	170	H (21), P (9)	LWR (30), WHR (1)	RS, SF	XW, MG
<i>Dc</i>	799	H (central)	LWR	YSS (OP)	XY
<i>Nb</i>	35	H (30), P (11), L (4), O (3)	LWR (43), WHR (2), OR (3)	YSS, SH, SF, RS	XW, XY, MG
<i>Ec</i>	4280	H (southern)	LWR	RS (OP)	XW
<i>Df</i>	350	H (11), (so.), P (2)	LWR	YSS (OP)	XY
<i>Wc</i>	37	H (15), P (8)	LWR	YSS, SH, SF	XY, MG
<i>Hc</i>	539	H (31), P (3)	LWR (30), PU (1)	RS (OP)	XW

* Species code, see Table 1 for complete names.

** H = Highlands; P = Polk; L = Lake; O = Orange.

‡ LWR = Lake Wales Ridge; WHR = Winter Haven Ridge; OR = Orlando Ridge; PU = Polk Upland.

‡‡ RS = rosemary scrub; YSS = yellow sand scrub; SF = scrubby flatwoods; SH = sandhill; (OP) = open microsites only.

*** XW = xeric white; XY = xeric yellow; MG = mesic gray.

(Nei 1978) were high for all species (Table 1). Values ranged from 0.94 for *H. cumulicola* to 0.99 for *D. frutescens*.

Distributions, Population Sizes, and Habitat Specificity

All seven species are endemic to central Florida (mainly along the LWR; Figure 2, Table 2) and are endangered mainly by habitat loss (USFWS 1998). *Dicerandra christmanii* has the narrowest range, confined to five small populations within a few kilometers of one another on the central LWR. *Eryngium cuneifolium* is restricted to the southern end of the LWR. *Dicerandra frutescens* is found mainly on the southern LWR with disjunct and morphologically distinct populations on the northern LWR in Polk County (N. Bissett, pers. comm.). *Hypericum cumulicola* and *L. ohlingerae* occupy the southern 2/3 of the LWR. *Nolina brittoniana*'s distribution extends north and east onto the Orlando Ridge, west onto the Winter Haven Ridge, and was historically reported from a disjunct site in Hernando County (Florida Natural Areas Inventory 1989). *Warea carteri* is found along the full length of the LWR. Historically, *W. carteri* was also known from the Atlantic Coastal (Brevard County) and Miami Rock Ridges (Broward and Dade Counties, Florida Natural Areas Inventory 1989), although neither of these areas currently supports this species.

Populations occur discontinuously across the species' ranges since suitable habitat is naturally patchily distributed and now increasingly fragmented by development. In addition, not all apparently suitable habitat patches are occupied, adding to the discontinuity in population distributions (e.g., *Hypericum cumulicola*, Quintana-Ascencio et al. 1998). Where plants are found, however, all species can occur in locally dense concentrations. Population sizes vary within and across species, being generally in the dozens of individuals for *N. brittoniana* and *W. carteri*, several hundred for *L. ohlingerae*, *D. frutescens*, and *H. cumulicola*, and often in the thousands for *E. cuneifolium* (Table 2). These population sizes may be partly a consequence of fire suppression or other recent historical factors and may not be typical of historical abundance patterns that genetic surveys reflect (Prober et al. 1998).

All species are restricted to excessively well-drained soils of xeric uplands and are more or less specialists for scrub or scrub and sandhill vegetation types (Table 2, see Abrahamson et al. 1984 and Menges 1999 for habitat descriptions). *Eryngium cuneifolium* and *H. cumulicola* are restricted to xeric white sands of rosemary scrub (Menges and Kimmich 1996, Quintana-Ascencio and Morales-Hernandez 1997). *Dicerandra christmanii* and *D. frutescens* are found only in openings in yellow-sand scrub (Abrahamson's southern ridge sandhill; Menges 1992, Menges et al. 1999). *Liatrix ohlingerae*, *N. brittoniana* and *W. carteri* are less specialized:

Table 3. Life history traits of seven endemic species of the Lake Wales and adjacent ridges

Sp*	Est. Max. Lifespan (years)	Propagule Dis-persal** (m)	Postfire Response	Breeding System	Pollinators/Movements
<i>Lo</i>	>10	0.66	Resprouter	Outcrossed	Butterflies/Long
<i>Dc</i>	5–10	1.32	Obligate seeder	Mixed	Bee Fly/Long
<i>Nb</i>	>10	(6.53)**	Resprouter	Outcrossed	Generalists/Long
<i>Ec</i>	5–10	1.32 (1.36)	Primarily Seeder†	Mixed	Generalists/variable
<i>Df</i>	5–10	1.30 (††)	Obligate seeder	Mixed	Bee Fly/Long
<i>Wc</i>	1	1.89	Obligate seeder	Mixed, High Self	Generalists/Variable
<i>Hc</i>	5–10	0.62 (0.95)	Obligate seeder	Mixed	Specialists/Short

* Species code, see table 1 for complete names.

** Estimated horizontal distance of primary propagule dispersal in meters, using data from laboratory trials in still air (Menges et al. 1998). Seeds are the main dispersal propagule for most species. Fruit disperse in *Nolina brittoniana*. For *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Dicerandra* spp., both seed dispersal and fruit dispersal (distance in parentheses) are possible. Wind dispersal for *Liatrix ohlingerae* may take propagules further.

† Very weak resprouter.

†† Fruits also disperse, but not as far as seeds (Finer and Menges, in prep.)

L. ohlingerae is found in scrubby flatwoods and rosemary scrub, while *N. brittoniana* is in both of these habitats plus xeric hammocks and sandhills. *Warea carteri* occurs in sandhills, scrubby flatwoods, and yellow-sand scrub.

Life History Characteristics

All species, except the annual *W. carteri*, are perennial herbs with moderate (on the order of 5–10 years) to long life spans (*L. ohlingerae*, *N. brittoniana*; Table 3). *Nolina brittoniana* and *L. ohlingerae* are resprouters with relatively stable demography and low annual turnover (Thomas et al. 1998, Menges unpubl.; Herndon, pers. comm.). The other five species rarely survive aboveground disturbances such as fire (Menges and Kohfeldt 1995) and, therefore, have lower demographic stability. Of these five, the four perennials (*E. cuneifolium*, *H. cumulicola*, *D. frutescens*, and *D. christmanii*) exhibit high turnover and are sensitive to post-disturbance community development (Menges 1992, Menges and Kimmich 1996, Quintana-Ascencio and Morales-Hernandez 1997, Menges et al. 1999). The annual *W. carteri* demonstrates the most pronounced population fluctuations, which in natural sites are closely tied to the occurrence of fire (Menges and Gordon 1996).

Breeding systems and pollinator movements vary among these seven species (Table 3). *Dicerandra christmanii*, *D. frutescens*, *H. cumulicola*, *E. cuneifolium* and *W. carteri* have at least some degree of mixed mating systems, with selfing relatively common in *W. carteri* (Evans et al. 2000) and inbreeding depression evident in *D. frutescens* (Menges et al. 1998). On the other hand, *N. brittoniana* is subdioecious and *L. ohlingerae* is an obligate outcrosser (Menges et al. 1998). Pollinator movements are probably very limited in *H. cumulicola*, which is visited by solitary trap-lining bees, but may include longer distances in *L. ohlingerae*, which is butterfly pollinated (Menges et al. 1998). The other species are pollinated either by suites of specialists that include wide-ranging insects, or by locally-abundant, strong-flying specialists, and probably have intermediate pollen movements.

None of the study species are specialized for animal-mediated seed dispersal. Estimated primary seed dispersal in still air was under 1.5 m in five of the six species, but was somewhat longer in *N. brittoniana* (Table 3). Secondary dispersal by wind and water may be important in such species as *L. ohlingerae* (field observations) and *D. frutescens* (Finer and Menges, in prep.), but is unlikely to move seeds much beyond a few meters from the parent plant.

Genetic Diversity Rankings Among Species

A comparison of genetic variation with life history factors indicates a concordance of 4 of 8 life history traits with genetic variation. In general, genetic variation was greatest in longer-lived, demographically stable, outcrossing species with greater pollinator movements. For the

Table 4. Comparisons of ranking of genetic variation (expected heterozygosity; H_e ; Table 2) and rankings of eight factors that could influence genetic variation for six scrub plants sampled from multiple populations. Highest values (predicted to be correlated with higher genetic variation) are indicated by "1" in the rankings. See notes for information on each ranking

Species Code (Table 1)	H_e	Life Span	Breeding System	Demographic Stability	Pollination	Seed Dispersal	Population Size	Range	Habitat Specialization
<i>Lo</i>	1	1	1	1	1	4	4	2	2
<i>Nb</i>	2	1	1	1	1	1	6	1	1
<i>Ec</i>	3	2	2	2	2	3	1	6	4
<i>Df</i>	4	2	2	2	1	3	3	4	4
<i>Wc</i>	5	3	3	3	2	2	5	3	2
<i>Hc</i>	6	2	2	2	3	4	2	5	3

NOTES

Life span: 1 = long-lived perennial; 2 = short-lived perennial; 3 = annual (Table 3).

Breeding System: 1 = outcrossing; 2 = mixed; 3 = mixed, primarily inbreeding (Table 3).

Demographic Stability: 1 = resprouter; 2 = perennial seeder; 3 = annual seeder (Table 3).

Pollination: 1 = generalist, long-distance; 2 = generalist, mixed distances; 3 = specialist, short-distance (Table 3).

Seed Dispersal: 1: >5 m; 2: 1.5–2 m; 3: 1–1.5 m; 4: 0–1 m (Table 3).

Population Size: Median population size rank (Table 2).

Range: Ranking for geographic range (1 = widest; 6 = narrowest).

Habitat Specialization: 1 = found in 3 types of vegetation, 3 groups of soils; 2 = found in 2 types of vegetation, 2 groups of soils; 3 = found primarily in one type of vegetation, one group of soil; 4 = restricted to one type of vegetation, one group of soil. Vegetation types for this classification are yellow-sand scrub, rosemary scrub, scrubby flatwoods, and sandhill. Soil groups for this classification are listed in Table 2.

six species with genetic data from multiple populations, the rankings of expected heterozygosity were consistent with life span, demographic stability, outcrossing, and pollinator movements (Table 4). In each case, the concordance of rankings was nearly perfect. Rankings for four other factors (seed dispersal, median population size, geographic range, and habitat specificity) were inconsistent with the rankings for genetic variation (Table 4).

For the four factors with nearly concordant rankings with expected heterozygosity, each had one inconsistency. Three of the four life-history inconsistencies included *W. carteri*, which was predicted to have lower genetic variation than *H. cumulicola* on the basis of its shorter life-span, less-stable demography, and tendency for inbreeding. These two species were correctly ranked on the basis of pollinator movements (being shorter in *H. cumulicola*). *D. frutescens* was predicted to have higher genetic variation than *E. cuneifolium* because it may have proportionately more longer-distance pollinator movements, although exact pollinator movement distances are poorly known. In actuality, *D. frutescens* had lower expected heterozygosity than *E. cuneifolium* (Table 4).

DISCUSSION

Comparative Genetics of Scrub Plants

Genetic variation is often correlated with a particular set of life-history traits (e.g., Loveless and Hamrick 1984, Hamrick et al. 1991, Gitzendanner and Soltis 2000). One would expect low genetic variation in our seven study species due to their narrow ranges, relatively short lifespans, limited seed dispersal, and (for five of seven species) self-compatible breeding systems. Of these species, only *Nolina brittoniana* has more than two of the traits associated with high genetic diversity.

Accordingly, we found low genetic diversity. Among our seven study species, six of seven have lower expected heterozygosity than most plant species and all had lower expected heterozygosity than the mean than published means for species with similar ecological traits (Hamrick and Godt 1989). Other genetic statistics were also generally lower than found in comparable plant groups.

Liatris ohlingerae was one of three species in our study with higher H_e than the published mean for narrow endemics, and with relatively high values for two other genetic statistics, although still below the all-species means. Its outcrossing, self-incompatible breeding system would predict high genetic diversity (Hamrick et al. 1991). *Liatris ohlingerae* is pollinated by highly mobile butterflies, which could create high gene flow, mixing all but the most isolated populations. Accordingly, *L. ohlingerae* was one of two study species with a lower F_{ST} value than the comparable literature mean. Similarly, the endemic *Liatris hellii* maintained fairly high levels of genetic diversity, although its populations were somewhat differentiated (Godt and Hamrick 1996).

Because *N. brittoniana* has a number of life history traits (long-lived, outcrossing, dioecious, relatively widespread, relatively well dispersed) often associated with high genetic variation, we expected this species to be highly variable. However, small local population sizes combined with clonal growth may act to limit genetic variation. *Nolina brittoniana* has the third highest level of genetic diversity of all the study species (Table 1). We detected no unique alleles in *N. brittoniana*, but we did find some suggestion of population differentiation based on local alleles and clines in allele frequencies (Dolan et al., in prep.).

Dicerandra christmanii has a surprisingly high level of genetic diversity ($H_e = 0.088$). Factors that would have predicted low variation include its extremely limited distribution (Huck et al. 1989), microhabitat specificity (Menges et al. 1999), and ability to set seed with self pollen (Menges et al. 1998). Small populations may be isolated in small patches of suitable microhabitats. Selfing and inbreeding among these few plants would be likely, which would tend to decrease heterozygosity. Although capable of selfing, *D. christmanii* is predominantly an outcrosser (Huck 1987, Menges et al. 1998). Genetic variation may therefore reflect the large population sizes and predominant outcrossing in large, contiguous habitat fragments before widespread habitat fragmentation (Prober et al. 1998).

The other study species have various life history traits but very low genetic variation ($H_e < 0.06$). For both *D. frutescens* and *Eryngium cuneifolium*, we sampled the majority of known populations, but found low levels of genetic variation. Variation in *E. cuneifolium* differed between our study (16 populations, 21 loci) and a prior survey of 2 populations with 31 loci (McDonald and Hamrick 1996; see discussion in Dolan et al. 2000). Our study of 13 *D. frutescens* populations (18 loci) detected consistently lower levels of genetic variation than found by McDonald and Hamrick (1996) in 2 populations, 17 loci.

Both *D. frutescens* and *E. cuneifolium* had unique alleles (Yahr et al., in prep.). The intermediate level of F_{ST} in *E. cuneifolium* (0.445) is accompanied by its high number of locally rare alleles (found in fewer than five populations at a frequency less than or equal to 0.1; Yahr et al., in prep). Gene flow in *E. cuneifolium* may occur infrequently enough to keep these often large, but frequently isolated populations, relatively differentiated.

Dicerandra frutescens on the southern LWR, with almost no population differentiation ($F_{ST} = 0.031$), was historically distributed more or less contiguously along a high yellow-sand ridge that has only been fragmented within the last 40–60 years. This historical distribution presumably would have permitted a substantial level of gene flow among populations. In addition, the bee-fly pollinator of *D. frutescens*, *Exprosopa fasciata* (Diptera; Bombyliidae), is a long distance flier and may have once been responsible for long distance pollen movements (Deyrup and Menges 1997). One *D. frutescens* population with a rare allele, found in the disjunct northern part of its range, may be part of a separate subspecies (N. Bissett, pers. comm.).

Whereas all the other species are perennial herbs with lifespans of at least 5–10 years, *Warea carteri* is an annual. Although its populations can persist for years within a seed bank, aboveground populations tend to be somewhat transient, peaking after fire or some kinds of mechanical disturbance and often subsequently disappearing aboveground (Menges and Gordon 1996). Dramatic annual and fire-related population size fluctuations may help explain low population differentiation (low F_{ST}) and low genetic diversity. Many populations likely remain unsampled since they are located only as a seed bank belowground. *Warea carteri* has two alleles with north-south clinal patterns (Evans et al. 2000).

Hypericum cumulicola had the lowest H_e of any species in this study, but with relatively

high levels of population differentiation within (Quintana-Ascencio et al. 1998) and among populations ($F_{ST} = 0.724$, also Dolan et al. 2000). These values indicate that there could be additional undetected alleles within both sampled and unsampled sites. Of the 34 populations sampled, we found rare or unique alleles in over half (Yahr et al., in prep.). This differentiation may result from very limited pollinator movement and hence gene flow among populations. Sytsma and Schaal (1985) hypothesized that the genetic structure of *Lisianthus skinneri*, a plant with a similar combination of self compatibility, short pollinator movements and high population differentiation, may be a result of founder populations and the strong influence of drift. Similarly, breeding system and pollination mode explained allozyme variation among three herbs species in an agricultural landscape in Norway (Berge et al. 1998).

Several factors were associated with differences in genetic variation among the six species sampled from multiple populations. Genetic diversity was highest for longer-lived perennials, species with stable demography, outcrossing species, and species with greater pollinator movements. Rankings of the six species for these four traits were almost perfectly ordered with rankings for H_e and other genetic statistics (Table 4). The combination of these four traits fits both *Liatris ohlingerae* and *Nolina brittoniana*. In particular, these two species can resprout following fire, so their population sizes are relatively stable through fire cycles. The four shorter-lived perennial plants and the annual *W. carteri* have strongly fluctuating population sizes through fire cycles, and may suffer bottlenecks due either to individual fires or fire suppression.

Population size, habitat specificity, geographic range, and primary seed dispersal were not related to the amount of genetic variation of populations or species. Although genetic variation is often positively associated with population size (e.g., Dolan 1994, Rajimann et al. 1994, Fischer and Matthies 1998, but see Shapcott 1994), the surveyed population sizes may be poor statistics for two reasons. First, because populations naturally fluctuate, our samples were not in stable demographic or genetic equilibrium. Habitat loss is also relatively recent (mainly in the 1900s, and accelerating since 1950). As a result, the distribution of alleles in the populations we sampled may be in flux, a hypothesis supported by the many loci we found that were not in Hardy-Weinberg equilibrium (Menges et al. 1998, Dolan et al. 2000). Similarly, in a survey of the relationship between within-species genetic variance and population size in 10 plant species, Ellstrand and Elam (1993) suggested that the three species that did not have a positive association were not in a stable genetic equilibrium. Finally, our definition of population boundaries was arbitrary, and we were unable to quantify plant densities in nearby patches, which may contribute to larger effective population sizes.

Current geographic range was poorly related to the overall levels of genetic variation among species in this study, consistent with studies of *Polygonella* species (Lewis and Crawford 1995). Factors other than geographic range often determine relative levels of genetic variation among species (Karron 1991). We also found no association of habitat specificity with narrow genetic variation, in contrast with expectations based on positive genetic/environmental correlations (Gray 1996) or strong selection imposed by unusual conditions (Aitken and Libby 1994).

Although long-distance seed dispersal may preserve overall genetic variation by keeping small populations connected to larger populations, six of our seven species have very limited seed dispersal (less than 2 m). The lack of variation in primary seed dispersal distances may account for its lack of association with genetic variation.

Gene flow probably varies among our study species, judging by variation in rare alleles (Yahr et al., in prep) and in F_{ST} , which can both be used to estimate gene flow (Slatkin 1985, Slatkin and Barton 1989). However, in cases with low gene flow and unsampled nearby populations, gene flow may be underestimated by an analysis of allele frequency since nearby unsampled populations could harbor the presumed unique alleles. Our sampling was designed to exclude all populations within 1.6 km of those that we sampled so we may have missed evidence of a stepping-stone model of gene flow between neighboring populations. Additionally, such models assume genetic equilibrium, a condition our sampled populations may not meet.

Implications for Conservation

While these seven species have generally low levels of genetic variation, our analyses suggest that there are important differences among some populations that could be related to adaptive traits allowing persistence under future, varying environments. As populations become further isolated by habitat fragmentation, the smallest populations may lose genetic variation and the species may lose rare or unique alleles [although effects of habitat fragmentation on genetic losses, differentiation, and gene flow may be unpredictable (Young et al. 1996)]. While some small populations should be protected to keep these rare alleles (Yahr et al., in prep.), species conservation may be best served by protecting larger areas that support groups of populations that can respond to spatial and temporal variation, including variation in the fire regime, without genetic impoverishment.

Our estimates of gene flow, inferred from distributions of genetic variation among populations and observations of pollinator movements, also may affect conservation decisions. Populations of *H. cumulicola* are apparently somewhat isolated, and preserved areas may need to be large enough to support genetically viable populations of this species. At the other extreme, *L. ohlingerae* apparently retains gene flow among sparsely-distributed patches of plants, mainly through long-distance pollinator movements.

These comparisons demonstrate that co-occurring narrowly endemic species can have a diversity of genetic patterns (see also Prober et al. 1990). Many factors (in the case of these Florida scrub species: life span, demographic stability, breeding systems, and pollinator movements) can potentially influence the amount and distribution of genetic variation. Because these species are phylogenetically unrelated, ranging two orders of magnitude in number of species per genus and with genera ranging in distribution from global to local (Willis 1973), their historical and biogeographic origins vary widely. These historical differences would contribute to observed differences in genetic patterns (Gitzendanner and Soltis 2000), despite apparently similar selective pressures (fire, naturally fragmented habitat, limited distribution, xeric soils).

It is unlikely that informed conservation decisions requiring detailed knowledge of genetic and demographic patterns can be made without direct study of the individual species of concern, especially for inbreeding species (Schoen and Brown 1991). Further loss of genetic variation due to habitat loss and fragmentation will impact the genetic variation of these species differently depending on their levels of genetic variation, spatial patterns in genetic variation, demographic traits, and levels of gene flow. Therefore, single conservation strategies are unlikely to achieve genetic conservation goals for suites of species.

ACKNOWLEDGMENTS

Funding for this study was provided by The Nature Conservancy's Ecosystem Research Program, the National Science Foundation (DEB 98-15370) and the Florida Division of Forestry. We thank Margaret Evans, Christine Hawkes, Jacqui Shaw, Andreas Erler, Craig Young, Stacey Halpern, Deborah Graves, Margie Mayfield, George Landman, Joyce Voneman, Dawn Berry, Pedro F. Quintana-Ascencio, Jose Luis Hierro, Christina M. Casado, Helen A. Violi, Kelly W. McConnell, Sanyaalak Burkhart, Owen D. Boyle, Satya Maliakal, Kurt O. Reinhart, Erica Goss, Matthew Finer, Patrick McIntyre, Abigail McCarthy, Philip Higuera, Molly Hunter, Carl Weekley, and Dorothy Mundell for their hard work. Roberta Pickert, Chris Casado, Scott Bergen, and Carl Weekley produced GIS analyses and maps. We are grateful to Margaret E.K. Evans for her excellent work with the breeding systems and pollinators of these species and Mark Deyrup for his insights into pollinator behavior and the ecology of Florida scrub in general. We also thank Christine Hawkes, Alan Herndon, Pedro F. Quintana-Ascencio, and Carl Weekley for providing information and insight on the ecology of our study species and the Florida Natural Areas Inventory for digital coverages and element occurrence records. We also appreciate the access given to populations by numerous public and private landowners. This manuscript was improved by the comments of Zack Murrell and Carl Weekley.

LITERATURE CITED

- ABRAHAMSON, W.G., A.F. JOHNSON, J.N. LAYNE, and P.A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Sci.* 47:209–250.
- AITKEN, S.N. and W.J. LIBBY. 1994. Evolution of the pygmy-forest edaphic subspecies of *Pinus contorta* across an ecological staircase. *Evol.* 48:1009–1019.
- BARRETT, S.C.H. and J.R. KOHN. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. *In: Falk, D.A. and K.E. Holsinger (eds.). Genetics and conservation of rare plants.* Oxford University Press, New York.
- BERGE, G., I. NORDAL, and G. HESTMARK. 1998. The effect of breeding system and pollination vectors on the genetic variation of small plant populations within an agricultural landscape. *Oikos* 81:17–29.
- BRADSHAW, A.D. 1994. Ecological significance of genetic variation between populations. p. 213–228. *In: Dirzo, R. and J. Sarakhan (eds.). Perspectives in plant population ecology.* Sinauer Associates, Sunderland, Massachusetts.
- BROOKS, H.K. 1981. Guide to the physiographic divisions of Florida. Florida Cooperative Extension Service, IFAS, University of Florida. 12 p. + map.
- BROWN, A.H.D. 1978. Isozymes, plant population genetic structure and genetic conservation. *Theor. Appl. Genet.* 52:145–157.
- BYERS, D.L. 1998. Effect of cross proximity on progeny fitness in a rare and a common species of *Eupatorium* (Asteraceae). *Amer. J. Bot.* 85:644–653.
- CARTER, L.J., D. LEWIS, L. CROCKETT, and J. VEGA. 1989. Soil survey of Highlands County, Florida. USDA Soil Conservation Service, Gainesville, Florida. 178 p. + maps.
- CESKA, J.F., J.M. AFFOLTER, and J.L. HAMRICK. 1997. Developing a sampling strategy for *Baptisia arachnifera* based on allozyme diversity. *Conserv. Biol.* 11:1133–1139.
- CHRISTMAN, S.P. and W.S. JUDD. 1990. Notes on plants endemic to Florida scrub. *Florida Sci.* 53:52–73.
- CLARK, A.M., B.W. BOWEN, and L.C. BRANCH. 1999. Effects of natural habitat fragmentation on an endemic scrub lizard (*Sceloporus woodi*): an historical perspective based on mitochondrial DNA gene genealogy. *Molecular Ecol.* 8:1093–1104.
- DEYRUP, M. and R. FRANZ. 1994. Rare and endangered biota of Florida. IV. Invertebrates. University Press of Florida, Gainesville.
- DEYRUP, M.A. and E.S. MENGES. 1997. Pollination ecology of the rare scrub mint *Dicerandra frutescens* (Lamiaceae). *Florida Sci.* 60:143–157.
- DOBSON, A.P., J.P. RODRIGUEZ, W.M. ROBERTS, and D.S. WILCOX. 1997. Geographic distribution of endangered species in the United States. *Science* 275:550–553.
- DOLAN, R.W. 1994. Patterns of isozyme variation in relation to population size, isolation, and phylogeographic history in royal catchfly (*Silene regia*; Caryophyllaceae). *Amer. J. Bot.* 81:965–972.
- DOLAN, R.W. 1995. The rare, serpentine endemic *Streptanthus morrisonii* (Brassicaceae) species complex, revisited using isozyme analysis. *Madrono* 20:338–346.
- DOLAN, R.W., R. YAHR, and E.S. MENGES. 2000. Conservation implications of genetic variation in three rare species endemic to Florida rosemary scrub. *Amer. J. Bot.* 86:1556–1562.
- DOLAN, R.W., E.S. MENGES, and R. YAHR. In prep. Genetic variation in *Nolina brittoniana*, a plant endemic to the central ridges of Florida. *J. Heredity*.
- ELLSTRAND, N.C. and D.R. ELAM. 1993. Population genetic consequences of small population size: implications for plant conservation. *Ann. Rev. Ecol. Syst.* 24:217–242.
- ESRI. 1996. Arc-View GIS 3.2. Environmental Systems Research Institute, Redlands, California.
- EVANS, M.E.K., R.W. DOLAN, E.S. MENGES, and D.R. GORDON. 2000. Genetic diversity and reproductive biology in *Warea carteri* (Brassicaceae): a narrowly endemic Florida scrub annual. *Amer. J. Bot.* 87:372–381.
- FALK, D.A. 1991. Joining biological and economic models for conserving plant genetic diversity. *In: Falk, D.A. and K.E. Holsinger (eds.). Genetics and conservation of rare plants.* Oxford University Press, New York.
- FINER, M. and E.S. MENGES. In prep. Seed dynamics of the endemic Florida scrub mint, *Dicerandra frutescens*: implications for fire management.
- FISCHER, M. and D. MATTHIES. 1998. RAPD variation in relation to population size and plant fitness in the rare *Gentianella germanica* (Gentianaceae). *Amer. J. Bot.* 85:811–819.
- FLORIDA NATURAL AREAS INVENTORY. 1989. Matrix of habitats and distribution by county for rare/endangered species in Florida. Florida Natural Areas, Tallahassee.
- FORD, R.D., J.M. ROBBINS, JR., J.T. WERNER, D. COWHERD, C.N. GORDON, W.B. WARMACK, M.M. BROWN, K.W. MONROE, W.G. GEORGE, T. SANDERS, and P.M. BASCH. 1990. Soil survey of Polk County, Florida. USDA Soil Conservation Service, Gainesville, Florida. 235 p. + maps.

- FRANKEL, O.H., A.H.D. BROWN, and J.J. BURDON. 1995. The conservation of plant biodiversity. Cambridge University Press, Cambridge, England.
- GITZENDANNER, M.A. and P.S. SOLTIS. 2000. Patterns of genetic variation in rare and widespread plant congeners. *Amer. J. Bot.* 87:783–792.
- GODT, M.J.W. and J.L. HAMRICK. 1996. Genetic diversity and morphological differentiation in *Liatris helleri* (Asteraceae), a threatened plant species. *Biodiversity Conserv.* 5:461–471.
- GODT, M.J., B.R. JOHNSON, and J.L. HAMRICK. 1996. Genetic diversity and population size in four rare southern Appalachian plant species. *Conserv. Biol.* 10:796–805.
- GODT, M.J., T. RACE, and J.L. HAMRICK. 1997. A population genetic analysis of *Ziziphus celata*, an endangered Florida shrub. *J. Heredity* 88:531–533.
- GRAY, A. 1996. Genetic diversity and its conservation in natural populations of plants. *Biodiversity Letters* 3:71–80.
- HAMRICK, J.L. and M.J.W. GODT. 1989. Allozyme diversity in plant species. *In: Brown, A.H.D., M.T. Clegg, A.L. Kahler, and B.S. Weir (eds.). Plant population genetics, breeding, and genetic resources.* Sinauer Associates, Inc., Massachusetts.
- HAMRICK, J.L., M.J.W. GODT, D.A. MURAWSKI, and M.D. LOVELESS. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. p. 75–86. *In: Falk, D.A. and K.E. Holsinger (eds.). Genetics and conservation of rare plants.* Oxford University Press, New York.
- HUCK, R.B. 1987. Systematics and evolution of *Dicerandra* (Labiatae). *Phanerogamarum Monographiae Tomus XIX.* J. Cremer, Berlin. 343 p.
- HUCK, R.B., W.S. JUDD, W.M. WHITTEN, J.D. SKEAN, JR., R.P. WUNDERLIN, and K.R. DELANEY. 1989. A new *Dicerandra* (Labiatae) from the Lake Wales Ridge of Florida, with a cladistic analysis and discussion of endemism. *Syst. Bot.* 14:197–213.
- HUENNEKE, L.F. 1991. Ecological implications of genetic variation in plant populations. *In: Falk, D.A. and K.E. Holsinger (eds.). Genetics and conservation of rare plants.* Oxford University Press, New York.
- KARRON, J.D. 1991. Genetic variation and breeding systems in rare plants. p. 87–98. *In: Falk, D.A. and K.E. Holsinger (eds.). Genetics and conservation of rare plants.* Oxford University Press, New York.
- KRESS, W.J., G.D. MADDOX, and C.S. ROESEL. 1994. Genetic variation and protection priorities in *Ptilimnium nodosum* (Apiaceae), an endangered plant of the eastern United States. *Conserv. Biol.* 8:271–276.
- LEWIS, P.O. and D.J. CRAWFORD. 1995. Pleistocene refugium endemics exhibit greater allozymic diversity than widespread congeners in the genus *Polygonella* (Polygonaceae). *Amer. J. Bot.* 82:141–149.
- LOVELESS, M.D. and J.L. HAMRICK. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* 15:65–95.
- MARSHALL, D.R. and A.H.D. BROWN. 1975. Optimum sampling strategies on genetic conservation. p. 369–377. *In: Frankel, O.H. and J.G. Hawkes (eds.). Crop genetic resources for today and tomorrow.* International Biological Programme 2. Cambridge University Press, Cambridge, England. (As cited in Brown and Briggs 1991.)
- MCDONALD, D.B. and J.L. HAMRICK. 1996. Genetic variation in some plants of Florida scrub. *Amer. J. Bot.* 83:21–27.
- MENGES, E.S. 1992. Habitat preferences and response to disturbance for *Dicerandra frutescens*, a Lake Wales Ridge (Florida) endemic plant. *Bull. Torrey Bot. Club* 119:308–313.
- MENGES, E.S. 1997. Evaluating extinction risks in plant populations. p. 49–65. *In: Fiedler, P.L. and P.M. Kareiva (eds.). Conservation biology for the coming decade.* Chapman and Hall, New York. 533 p.
- MENGES, E.S. 1999. Ecology and conservation of Florida scrub. p. 7–22. *In: Anderson, R.C., J.S. Fralish, and J. Baskin (eds.). Savannas, barrens, and rock outcrop communities of North America.* Cambridge University Press, New York.
- MENGES, E.S., R.W. DOLAN, D.R. GORDON, M.E.K. EVANS, and R. YAHR. 1998. Demography, ecology, and preserve design for endemic plants of the Lake Wales Ridge, Florida. Final Report to The Nature Conservancy's Ecosystem Research Program.
- MENGES, E.S. and D.R. GORDON. 1996. Three levels of monitoring intensity for rare plant species. *Nat. Areas J.* 16:227–237.
- MENGES, E.S. and C.V. HAWKES. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecol. Appl.* 8:935–946.
- MENGES, E.S. and J. KIMMICH. 1996. Microhabitat and time-since-fire: effects of demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. *Amer. J. Bot.* 83:185–191.
- MENGES, E.S. and N. KOHFELDT. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bull. Torrey Bot. Club* 122:282–297.
- MENGES, E.S., P.J. MCINTYRE, M.S. FINER, E. GOSS, and R. YAHR. 1999. Microhabitat of the narrow Florida

- scrub endemic *Dicerandra christmanii*, with comparisons to its congener *D. frutescens*. J. Torrey Bot. Club 126:24–31.
- NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.
- OOSTERMEIJER, J.G.B., M.W. VAN EIJCK, N.C. VAN LEEUWEN, and J.C. M. DEN NIJS. 1995. Analysis of the relationship between allozyme heterozygosity and fitness in the rare *Gentiana pneumonanthe*. J. Ecol. 84:153–166.
- PARKER, K.C. and J.L. HAMRICK. 1996. Genetic variation in sand pine (*Pinus clausa*). Can. J. For. Res. 26: 244–254.
- PERONI, P.A. and W.G. ABRAHAMSON. 1985. A rapid method for determining losses of native vegetation. Nat. Areas J. 5:20–24.
- PETIT, R.J., A. EL MOUSADIK, and O. PONS. 1998. Identifying populations for conservation on the basis of genetic markers. Conserv. Biol. 12:844–855.
- PROBER, S.M., C. TOMPKINS, G.F. MORAN, and J.C. BELL. 1990. The conservation genetics of *Eucalyptus paliformis* L. Johnson et Blaxell and *E. parvifolia* Cambage, two rare species from south-eastern Australia. Austr. J. Bot. 38:79–95.
- PROBER, S.M., L.H. SPINDLER, and A.H.D. BROWN. 1998. Conservation of the grassy white box woodlands: effects of remnant population size on genetic diversity in the allotetraploid herb *Microseris lanceolata*. Conserv. Biol. 12:1279–1290.
- QUINTANA-ASCENCIO, P.F. and M. MORALES-HERNANDEZ. 1997. Fire-mediated effects of shrubs, lichens and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. Oecologia 112:263–271.
- QUINTANA-ASCENCIO, P.F., R.W. DOLAN, and E.S. MENGES. 1998. *Hypericum cumulicola* demography in unoccupied and occupied Florida scrub patches with different time-since-fire. J. Ecol. 86:640–651.
- RAIJMANN, L.E.L., N.C. VAN LEEUWEN, R. KERSTEN, J.G.B. OOSTERMEIJER, H.C.M. DEN NIJS, and S.B.J. MENKEN. 1994. Genetic variation and outcrossing rate in relation to population size in *Gentiana pneumonanthe* L. Conserv. Biol. 8:1014–1026.
- SCHEMSKE, D.W., B.C. HUSBANDS, M.H. RUCKELSHAUS, C. GOODWILLIE, I.M. PARKER, and J.G. BISHOP. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.
- SCHOEN, D.L. and A.H.D. BROWN. 1991. Intraspecific variation in population gene diversity and effective population size correlates with mating system in plants. PNAS 88:4494–4497.
- SHAPCOTT, A. 1994. Genetic and ecological variation in *Atherosperma moschatum* and the implications for conservation of its biodiversity. Aust. J. Bot. 42:663–686.
- SLATKIN, M. 1985. Rare alleles as indicators of gene flow. Evol. 39:53–65.
- SLATKIN, M. and N.H. BARTON. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evol. 43:1349–1368.
- SUN, M. 1996. Effects of population size, mating system, and evolutionary origin on genetic diversity in *Spiranthes sinensis* and *S. hongkongensis*. Conserv. Biol. 10:785–795.
- SWOFFORD, D.L. and R.B. SELANDER. 1989. Biosys-1: A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey, Champaign.
- SYTSMAN, K.J. and B.A. SCHAAL. 1985. Genetic variation, differentiation, and evolution in a species complex of tropical shrubs based on isozyme data. Evol. 39:582–593.
- THOMAS, K., J. SLAPCINSKY, and D.R. GORDON. 1998. Monitoring report: *Nolina brittoniana*. Unpublished, The Nature Conservancy, Gainesville, Florida.
- USFWS. 1998. Multi-species recovery plan for the threatened and endangered species of south Florida. Volume I. The species. Technical/Agency Draft. Vero Beach, Florida.
- WHITE, W.A. 1970. The geomorphology of the Florida peninsula. Florida Department of Natural Resources, Tallahassee.
- WILLIS, J.C. 1973. A manual and dictionary of the flowering plants and ferns, 8th ed. (revised by H.K. Airy Shaw). Cambridge University Press, Great Britain.
- WRIGHT, S. 1951. The genetic structure of populations. Ann. Eugenics. 15:323–354.
- WRIGHT, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evol. 19:395–420.
- WRIGHT, S. 1977. Evolution and the genetics of population. Volume 3. Experimental results and evolutionary deductions. University of Chicago Press, Chicago, Illinois.
- YAHR, R., E.S. MENGES, R.W. DOLAN, and D.R. GORDON. In prep. Do preserves protect genetic diversity? An evaluation using a survey of genetic structure of seven endemic plants on Florida's Lake Wales Ridge.

- YOUNG, A.G., A.T. BOYLE, and T. BROWN. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* 11:413–418.
- YOUNG, A.G. and A.H.D. BROWN. 1996. Comparative population genetic structure of the rare woodland shrub *Daviesia suaveolens* and its common congener *D. mimosoides*. *Conserv. Biol.* 10:1220–1228.
- YOUNG, A.G., A.H.D. BROWN, and F.A. ZICH. 1999. Genetic structure of fragmented populations of the endangered daisy *Rutidosia leptorrhynchoides*. *Conserv. Biol.* 13:256–265.