

Microhabitat of critically endangered *Lupinus aridorum* (Fabaceae) at wild and introduced locations in Florida scrub

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Abstract Elucidating microhabitat preferences of a rare species are critical for its conservation. *Lupinus aridorum* McFarlin ex Beckner (Fabaceae) is a critically endangered plant known only from a few locations in imperiled Florida scrub habitat and nothing is known about its preferred microhabitat. Our goals were three-fold. First, determine whether *L. aridorum* has multiple cytotypes because this can influence its spatial distribution. Second, measure how microhabitat characteristics at locations supporting wild *L. aridorum* vary from random locations, which will provide information about microhabitat characteristics that influence the spatial distribution of individuals. Third, measure whether microhabitat characteristics differ between locations supporting wild or introduced plants, which will provide information about the realized and fundamental niche.

Our research determined that *L. aridorum* is diploid and grew, on average, in areas closer to trees and shrubs, with lower soil moisture, and with a greater mixture of detritus than random locations. Some microhabitat characteristics at locations where *L. aridorum* were introduced were similar to microhabitat supporting wild *L. aridorum*, but multiple soil characteristics differed as did the plant community, which contained more non-native plant species near introduced plants. Therefore, the realized niche is narrower than the fundamental niche. Overall, information about the microhabitat of *L. aridorum* can be used to design appropriate management programs to conserve and restore populations of this plant species and species that occupy a similar niche in imperiled Florida scrub.

Keywords Cytotype · Gap specialist · Niche · Scrub lupine · Soil · Spatial distribution

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Introduction

The most common threat to the persistence of species worldwide is loss of habitat (Wilcove et al. 1998; Venter et al. 2006), but there are efforts to slow or stop the loss of habitat. One method to conserve species is to identify and conserve biodiversity hotspots that contain populations of many rare species (Myers et al. 2000). Approximately 60,000 plant species remain unknown to science and are predicted to be endemic primarily to biodiversity hotspots (Joppa et al. 2011).

The preferred microhabitat of a species is a major factor controlling population and community dynamics of plants (e.g., Münzbergová 2005; Richardson and Hanks 2011); therefore, elucidating the microhabitat of a rare species within these biodiversity hotspots is critical for its conservation.

Florida scrub is one of the most imperiled habitats in North America, is found on xeric sandy ridges, and is a biodiversity hotspot for endemic plants, containing one of the highest concentrations of endemic plants in the Southeastern United States (Estill and Cruzan 2001). Twenty-nine of these endemic species are federally listed as threatened or endangered. Most short-lived perennial plants in Florida scrub are gap specialists (Christman and Judd 1990; Petru and Menges 2003; Richardson et al. 2013) and depend on frequent disturbance, such as fires and hurricanes, to maintain openings in the overstory and sandy gaps in the understory. Survival and reproductive effort of gap specialists normally peak a few years after disturbance before mortality then increases with increasing time postdisturbance (Ostertag and Menges 1994; Menges and Quintana-Ascencio 2004; Menges et al. 2006; Evans et al. 2008) because gap specialists in Florida scrub may be sensitive to variation in characteristics of their habitat, especially the amount of competitors, detritus, and canopy cover (Peterson et al. 2013; Richardson et al. 2013). Plant species endemic to Florida scrub are presumed to be rare because they are adapted to this specific type of habitat. The fundamental niche, which is the full range of environmental conditions and resources an organism can occupy and use, of these plant species is likely contained entirely within Florida scrub. However, there is evidence that the realized niche (i.e., the range of environmental conditions actually used by a species) of some species in Florida scrub currently is narrower than the fundamental niche (Richardson et al. 2013). Therefore, rare plant species may have additional resources that they are currently not exploiting, but could be used to support the establishment and growth of populations.

Lupinus aridorum McFarlin ex Beckner (Fabaceae) was first described in 1982 (Beckner 1982), but little is known about its biology and ecology. *L. aridorum* is one of the most critically endangered plant species in Florida, occupying only two ridges in

central Florida. Based on the fact that *L. aridorum* occupies Florida scrub and is a short-lived perennial that only grows up to 1 m tall, it is likely a gap specialist, but nothing has been reported in the primary literature about its preferred microhabitat. The species could be found at 15 sites in central Florida when it was listed under the Endangered Species Act (USFWS 1987), but is now only found at nine sites in Polk and Orange Counties. A population at one of these sites has been augmented with germplasm propagated at Bok Tower Gardens, BTG (Lake Wales, FL) as part of a program to conserve this species. Two populations of *L. aridorum* also were introduced at new sites and one was introduced at a site of an extinct population. However, the populations at these sites are small (1–300 individuals in historic locations and 25–475 in new populations) and wild populations are mostly declining in size and restricted to small fragmented areas (0.1–1 ha) that are not managed for this plant species, so they are at risk of local extinction.

Population size and the spatial distribution may be restricted, in part, if seed dispersal is limited by intrinsic or extrinsic factors (Eriksson and Ehrlén 1992; Orrock et al. 2006) and/or if suitable habitat is limiting (Graae et al. 2011; Dybzinski and Tilman 2012). If *L. aridorum* has multiple cytotypes, this also may influence its spatial distribution because cytotypes of a plant species may occupy different macrohabitats or microhabitats (Stuessy et al. 2004; Richardson and Hanks 2011). Therefore, our goals were threefold. First, determine whether *L. aridorum* has multiple cytotypes. Second, use three sites to determine how microhabitat characteristics at locations supporting wild *L. aridorum* plants vary from random locations. This will provide information on microhabitat characteristics that may influence the spatial distribution of *L. aridorum*. Third, use five sites to determine whether microhabitat characteristics differ between locations supporting wild or introduced plants, which will provide information about the realized and fundamental niche. Ultimately, this information can be used by land managers and restoration practitioners to identify factors that may threaten or promote survival, microhabitat that needs to be conserved or restored, and microhabitat suitable to introduce populations of *L. aridorum*.

Methods

Study sites

Specific names and geographical locations of the five study sites are not given to protect the remaining populations of *L. aridorum*. Information about the sites is given in Table 1, but we provide additional details here. The sites all had sandy, well-drained acidic (mean pH 4.4) soil that supported Florida scrub habitat. The soil is primarily St. Lucie Series sand that is excessively deep and receives approximately 150 cm of rain per year. The canopy was relatively open and dominated by *Persea borbonia* (L.) Spreng., *Pinus* spp., and *Quercus* spp., although disturbances to maintain these gaps are infrequent because almost no management is done on sites supporting wild populations. We introduced seedlings that had been propagated at BTG to Sites 3–5 between 2008 and 2012 and tagged each plant with a unique identification number. The plants introduced at Site 3 came from seeds collected at Site 2, plants introduced at Site 5 came from seeds collected at Site 1, and plants at Site 4 came from seeds that had been collected from over a dozen sites and stored in the Center for Plant Conservation's National Collection at BTG. We chose Sites 3–5 to host populations because they represented some of the only scrub habitat remaining on protected land within the historical range of *L. aridorum*. The microhabitat was not disturbed when planting seedlings, except to dig holes that were approximately 10 cm wide. We measured microhabitat near introduced plants that had reached reproductive maturity and were as large as

wild plants to ensure that they were at least a couple of years old and were persisting in these new sites.

Determination of cytotype

We determined the cytotypic composition of three populations (Sites 1–3) of *L. aridorum* in February 2013. We chose these three populations because they were the most genetically diverse when assessed with microsatellites (Bupp 2013). We haphazardly chose 10 individuals from across a variety of microhabitats at each of the three sites ($N = 30$). Leaves from study plants were cytotyped by flow cytometry (following the methods of Stehlik et al. 2007) using a Beckman–Coulter Epics XL-MCL flow cytometer (Fullerton, California, USA) at Iowa State University to measure nuclear DNA content. Cytotype of *L. aridorum* was determined by measuring the fluorescence of propidium iodide (425 nm excitation) for ~3,000–5,000 nuclei from each plant and comparing it to two standards of *L. villosus* Willd., which is a diploid (Conterato and Schifino-Wittman 2006). All individuals of *L. aridorum* that we tested, and provided usable results, were diploid (see “Results” section), so our environmental measurements (see next section) did not have to account for differential spatial distribution due to the presence of cytotypes.

Environmental measurements

We tested for differences in microhabitat among wild, random, and introduced locations (hereafter “site” refers to the larger geographic area inhabited by a

Table 1 Five sites in central Florida, USA used to characterize microhabitat associated with wild and introduced populations of *Lupinus aridorum*

Sites (owner)	Hectares (occupied by <i>L. aridorum</i>)	Number of individuals	Type of location		
			Wild	Introduced (number introduced; year introduced)	Random
1 (USA)	14.0 (10.4)	910	x		x
2 (Orange County)	41.8 (2.3)	308	x		x
3 (City of Orlando)	72 (0.2)	133	x	x (1,317; 2010–2012)	x
4 (State of Florida)	26.3 (0.2)	350		x (1,263; 2008–2010)	x
5 (City of Lake Alfred)	14.1 (0.01)	100		x (1,221; 2010–2012)	x

Microhabitat was characterized at 20 locations for each type of population within a site and also at 20 corresponding random locations

population and “location” refers to a plot within a site used to characterize microhabitat) of *L. aridorum* by using the same environmental variables that we have previously used to characterize the structure of microhabitat (Richardson et al. 2006, 2013; Richardson and Hanks 2009, 2011). Random locations were selected by walking a randomly determined direction and number of paces (between 2 and 20 paces) from each wild and introduced plant and marked using a flag. We used a relatively small number of paces when determining random locations so that they were in proximity to the local population of *L. aridorum*. We measured the following microhabitat characteristics at each location ($N = 60$ wild, 60 introduced, and 100 random locations) in April 2013: (1) distance to the nearest overstory tree, (2) distance to the nearest woody shrub that was taller than *L. aridorum*, (3) soil moisture (i.e., percent relative saturation; Kelway® soil pH and moisture meter, Kel Instruments Co., Inc., Wyckoff, NJ), (4) canopy density (spherical densiometer, Robert E. Lemmon, Forest Densiometers, Bartlesville, OK), (5) number of woody stems within a 2 m² quadrat centered on the lupine or flag (not including the central lupine, but including other *L. aridorum*, if present), (6) species richness within the 2 m² quadrat (i.e., number of plant species), (7) maximum height of the understory vegetation within the 2 m² quadrat; and percentage of ground cover types within the 2 m² quadrat in which we quantified, (8) bare ground, (9) detritus, (10) grasses, (11) herbaceous plants (nongrasses), and (12) woody plants. We determined the percentage of ground cover types by calculating the area of each quadrat that they covered. This area was estimated visually and quantified by assigning units based on the following system (after Richardson and Hanks 2009): 0.5 (0–1 % of the total area of the quadrat), 3 (1–5 %), 15 (5–25 %), 37.5 (25–50 %), 62.5 (50–75 %), 85 (75–95 %), and 97.5 (95–100 %). At each location we also identified the species of the nearest overstory tree and midstory woody shrub, the species of the most abundant ground cover plant within the 2 m² quadrat, and the type of detritus within the 2 m² quadrat. Detritus at each location was classified into one of six groups (after Richardson et al. 2013): (1) no detritus, (2) decaying leaves from herbaceous plants, (3) decaying leaves from broadleaf woody plants, (4) pine needles, (5) twigs and branches, or (6) a mixture of groups 2–5.

We analyzed the composition of soil within the five study sites by collecting four samples each from near random locations or those supporting wild or introduced plants. However, samples were not collected at random locations at Site 5, which reduced our total sample size to 40. Soil samples were collected by slicing a core with a shovel to a depth of 15–20 cm. Samples were packaged in plastic bags and shipped to Agro Services International, Inc. (Orange City, FL) for analysis of pH, percent organic matter, soluble salts (ppm), calcium (meq/100 cm³), magnesium (meq/100 cm³), potassium (meq/100 cm³), nitrogen (µg/cm³), phosphorus (µg/cm³), sulfur (µg/cm³), boron (µg/cm³), copper (µg/cm³), iron (µg/cm³), manganese (µg/cm³), and zinc (µg/cm³).

How does microhabitat at locations supporting wild *L. aridorum* vary from random locations within Florida scrub?

We determined how microhabitat differed between 60 locations where plants were present and 60 locations where plants were absent at Sites 1–3 (Table 1) using Akaike’s information criterion adjusted for small sample sizes (AIC_c), and Akaike weights (w_i), which were calculated using the residual sums of squares from linear regressions, with location as the response variable and microhabitat characteristics as the regressor variables. This information-theoretic approach identifies the most parsimonious models from a set of candidate models, given the maximized log-likelihood of the fitted model. AIC_c is informative only if relevant predictor variables are used (Anderson 2008), so we selected four predictor variables for modeling (i.e., distance to the nearest overstory tree, distance to the nearest shrub, soil moisture, and the abundance of bare ground within the 2 m² quadrat). We chose these predictor variables because we thought they would be most likely to explain differences between wild and random locations based on our personal observations during data collection and preliminary analysis. The set of 15 candidate models included all combinations of the predictor variables. We used square-root, base-10 log, and square-root arcsine transformations on data when necessary to meet assumptions of normality prior to analysis. The final sample size was reduced from 120 to 114 because of some missing data. Differences between all 12 of the original microhabitat

characteristics near wild and random locations were also tested by general linear models (for continuous data) or negative binomial models (for count data) and were blocked by site, including the interaction term (PROC GLM or PROC GENMOD; SAS Institute 2011). The results from this more conventional statistical modeling verified that only the four predictor variables we selected for AIC_c modeling were significant. We present only the results for AIC_c modeling because the output is more informative (Anderson et al. 2000).

The ΔAIC_c value for each model is the relative level of empirical support compared to the model with the highest support (see Anderson 2008) and a value between 0 and 2 indicates strong support of the model. The weight of each model varies from 0 (no support) to 1 (complete support) and is the probability that it is the best model. The evidence ratio (Δ_i) is a quantitative measure of the strength of a model compared to the best model. Adjusted R^2 values indicate how well each model fits the data set and its relative efficacy as a tool for prediction. The relative importance of each predictor variable varies from 0 (no support) to 1 (complete support) and is calculated by summing the weight of each model in which the variable appears (Anderson 2008). Regression coefficients [\pm standard error (SE)] indicate whether predictor variables are positively or negatively associated with the response variable (i.e., presence of *L. aridorum*).

We calculated the percentage of times, four categories of overstory trees were the nearest tree to wild and random locations at Sites 1–3: (1) *P. borbonia*, (2) *Pinus* spp. [predominately *Pinus clausa* (Chapm. Ex Engelm.) Sarg.], (3) *Quercus* spp. (predominately *Q. geminata* Small), or (4) other species of trees. We calculated the percentage of times, five categories of shrubs were closest to wild and random locations: (1) *Ceratiola ericoides* Michx., (2) *Garberia heterophylla* (W. Bartram) Merr. and F. Harper, (3) *Quercus* spp. (predominately *Q. geminata*), (4) *Serenoa repens* (W. Bartram) Small, or (5) other species of shrubs. We also calculated the percentage of times, four categories of plants were the most abundant ground cover within the 2 m² quadrat at wild and random locations: (1) *Cladonia leporina* Fr., (2) grass spp., (3) *Polygonella polygama* (Vent.) Engelm. and A. Gray, and (4) other species. Lastly, we calculated the percentage of times each of the six categories of detritus was the dominant type at wild and random locations. Separate χ^2

contingency tests were used to determine whether the categories of trees, shrubs, ground cover plants, and detritus, calculated across the three sites, nearest to wild and random locations were different.

Differences between soil characteristics near wild and random locations were tested by general linear models blocked by site, including the interaction term (PROC GLM; SAS Institute 2011). We eliminated the interaction term when it was nonsignificant (see Milliken and Johnson 1984). We used square-root and base-10 log transformations on data when necessary to meet assumptions of normality prior to analysis. We present the mean and SE of the mean (SEM) of nontransformed data for soil characteristics and for all of the analyses in the following section.

How does microhabitat differ between locations with wild or introduced populations?

Differences between microhabitat and soil characteristics near introduced, wild, and random locations were tested by separate general linear models blocked by site, including the interaction term (PROC GLM; SAS Institute 2011). We eliminated the interaction term when it was nonsignificant. We used square-root and base-10 log transformations on data when necessary to meet assumptions of normality prior to analysis. Data that could not be transformed to achieve normality were analyzed with the *F*-approximation of the Friedman test and the associated Rank Sum multiple comparison test (PROC GLMMIX; SAS Institute 2011). Random locations used for these analyses were from Sites 3–5, which is also where we characterized the microhabitat of introduced populations. However, wild populations used for these analyses were from Sites 1–3, so the locations used to compare microhabitat associated with these two types of populations were largely from different sites (Table 1). We used general linear models for these analyses instead of modeling with AIC_c because AIC_c cannot determine whether two groups are different, but is appropriate for determining why two groups are different, as in our previous comparison between wild plants and random locations.

We used separate χ^2 contingency tests, as previously described, to compare the nearest tree and shrub and type of ground cover plants and detritus at introduced locations versus wild and random locations. However, some categories differed from the

previous analyses. Overstory trees were classified as: (1) *P. borbonia*, (2) *Pinus* spp., (3) *Quercus* spp., (4) other species of native trees, and (5) other species of nonnative trees. Shrubs were classified as: (1) *Quercus* spp., (2) *S. repens*, (3) *Sideroxylon tenax* L., or (4) other species of shrubs. Ground cover plants were classified as: (1) *C. leporina*, (2) grass spp., (3) *Paronychia chartacea* ssp. *chartacea* Fernald, (4) other native species, and (5) other nonnative species. We included a category for nonnative trees and ground cover plants because of their abundance near introduced plants.

Results

Determination of cytotype

We were able to unambiguously determine the cytotype for 29 of the 30 *L. aridorum*. The mean fluorescence of propidium iodide for *L. aridorum* was $43,101 \pm 1,149$ and the mean for *L. villosus* was $49,729 \pm 1,528$, which were not different ($\chi^2 = 2.03$, $P = 0.15$). Therefore, all plants that we tested were diploid.

How does microhabitat at locations supporting wild *L. aridorum* plants vary from random locations within Florida scrub?

Three models identifying differences in microhabitat between locations with wild *L. aridorum* and locations that were randomly selected are equally plausible because they had strong empirical support relative to the other models in the candidate set ($\Delta AIC_c < 2$;

Table 2). However, the adjusted R^2 values are low for the models, so the models do not strongly fit the data. The AIC_c model that had the greatest support indicated that *L. aridorum* was negatively associated with distance to the nearest overstory tree, distance to the nearest shrub, and soil moisture, and positively associated with the relative proportion of bare ground. The most important predictor variables (i.e., in nearly every model that carried weight) was distance to the nearest shrub and proportion of bare ground ($\Sigma w_i = 0.98$ and 0.93 , respectively). Wild plants were a mean (\pm SEM) distance of 195 ± 44 cm from shrubs and 62 ± 4 % of the surrounding ground was bare, whereas random locations were a mean distance of 401 ± 46 cm from shrubs and 51 ± 4 % of the ground was bare. Distance to the nearest tree and soil moisture may be moderately important predictor variables because these variables carried a moderate weight ($\Sigma w_i = 0.71$ and 0.54 , respectively). Wild plants were a mean distance of 541 ± 72 cm from trees and the surrounding soil had 0 ± 0 % moisture, whereas random locations were a mean distance of 862 ± 76 cm from trees and the surrounding soil had 0.4 ± 0 % moisture.

The type of most abundant ground cover plant did not differ between wild and random locations ($\chi^2 = 0.96$, $df = 3$, $P = 0.81$). Ground cover plants were very diverse at wild and random locations, but *C. leporina* was the most abundant species at nearly 30 % of the locations. However, the type of nearest tree, nearest shrub, and detritus differed between wild and random locations (tree, $\chi^2 = 15.5$, $df = 3$, $P < 0.001$; shrub, $\chi^2 = 21.2$, $df = 4$, $P < 0.001$; detritus, $\chi^2 = 15.51$, $df = 5$, $P = 0.01$). *Pinus* spp. were the most abundant tree near wild and random locations, but wild

Table 2 Best fit AIC_c models from 15 candidate models that explain differences in microhabitat of wild *Lupinus aridorum* and random locations with four explanatory variables: distance to the nearest overstory tree, distance to the nearest shrub, soil moisture, and the relative proportion of bare ground within a 2 m² quadrat

Model variables	<i>K</i>	Log (<i>L</i>)	ΔAIC_c	w_i	Δ_i	Adjusted R^2
Distance to overstory (-0.01 ± 0.00), distance to shrub (-0.02 ± 0.00), soil moisture (-0.51 ± 0.32), proportion of bare ground (0.32 ± 0.12)	6	91.2	0.0	0.37	1.0	0.16
Distance to overstory (-0.01 ± 0.00), distance to shrub (-0.02 ± 0.00), proportion of bare ground (0.38 ± 0.12)	5	89.9	0.3	0.31	1.2	0.15
Distance to shrub (-0.02 ± 0.00), proportion of bare ground (0.36 ± 0.12)	4	87.9	2.0	0.13	2.8	0.13

The regression coefficient \pm SE is given in parentheses for each variable

K number of parameters in the model, ΔAIC_c relative level of empirical support compared to the model with the highest support, w_i Akaike weights, Δ_i evidence ratio

Table 3 Relative frequency (\pm SEM) that shrub and tree species were nearest to locations of wild *Lupinus aridorum* and random locations and relative frequency (\pm SEM) that six categories of detritus were present at these locations across three sites in central Florida, USA

Locations	Tree species					
	<i>Persea borbonia</i>	<i>Pinus</i> spp.	<i>Quercus</i> spp.	Other spp.		
Wild	28.3 (11.7)	43.3 (3.3)	25.0 (11.5)	3.3 (1.7)		
Random	8.0 (4.0)	54.3 (8.7)	28.0 (4.9)	8.7 (4.7)		
	Shrub species					
	<i>Ceratiola ericoides</i>	<i>Garberia heterophylla</i>	<i>Serenoa repens</i>	<i>Quercus</i> spp.	Other spp.	
Wild	1.3 (1.3)	4.0 (4.0)	21.7 (14.9)	4.7 (3.7)	28.3 (8.8)	
Random	8.3 (6.0)	15.7 (15.7)	11.0 (8.6)	21.7 (18.3)	43.7 (14.4)	
	Detrital category					
	No detritus	Leaves of herbs	Leaves of broadleaf woody plants	Pine needles	Twigs/branches	Mixture of detritus
Wild	15.0 (0.0)	10.0 (2.9)	10.0 (5.7)	6.7 (6.7)	6.7 (6.7)	51.7 (7.3)
Random	39.0 (4.2)	9.7 (1.3)	9.7 (1.3)	5.3 (5.3)	5.3 (5.3)	33.7 (12.2)

L. aridorum were much more likely to be located near *P. borbonia* than were random locations (Table 3). Wild locations were associated with the shrub *S. repens* more often than random locations, and were less often associated with all other types of shrubs than were random locations (Table 3). Locations with wild *L. aridorum* most often had a mixture of detritus within 2 m², but random locations were commonly associated with no detritus (Table 3).

Percent organic matter, soluble salts, and iron differed near wild plants and random locations (organic matter, $F = 10.7$, $df = 1$, $P = 0.004$; salts, $F = 10.2$, $df = 1$, $P = 0.005$; iron, $F = 4.78$, $df = 1$, $P = 0.04$). Organic matter and soluble salts were higher in the soil near wild plants ($0.64 \pm 0.19\%$ and 28.1 ± 2.5 ppm, respectively) than random locations ($0.38 \pm 0.14\%$ and 21.3 ± 1.5 ppm, respectively). However, the amount of iron in the soil was lower near wild plants (40.5 ± 11.9 $\mu\text{g}/\text{cm}^3$) than random locations (89.9 ± 34.4 $\mu\text{g}/\text{cm}^3$).

How does microhabitat differ between locations with wild or introduced populations?

Statistical modeling indicated seven characteristics of the soil and six characteristics of the local plant community varied among wild, introduced, and

random locations, but there is a great deal of variation among the five field sites which makes interpretation of the data challenging (Table 4). In general, all features of the microhabitat that we measured were similar at introduced and random locations. Phosphorous, copper, iron, and pH were higher, on average, at locations with introduced *L. aridorum* versus wild plants, but the opposite was true for sulfur (Table 4A). Wild plants on average were closer to woody understory plants and shrubs than introduced plants (Table 4B).

The type of nearest tree, nearest shrub, ground cover, and detritus differed between introduced and wild locations of *L. aridorum* (tree, $\chi^2 = 19.8$, $df = 4$, $P < 0.001$; shrub, $\chi^2 = 15.7$, $df = 3$, $P < 0.001$; ground cover, $\chi^2 = 53.3$, $df = 4$, $P < 0.001$; detritus, $\chi^2 = 12.2$, $df = 5$, $P = 0.03$). The type of nearest shrub and ground cover also differed between introduced and random locations, but the nearest tree and detritus did not (tree, $\chi^2 = 5.1$, $df = 4$, $P = 0.28$; shrub, $\chi^2 = 8.8$, $df = 3$, $P = 0.03$; ground cover, $\chi^2 = 15.6$, $df = 4$, $P = 0.004$; detritus, $\chi^2 = 3.7$, $df = 5$, $P = 0.59$). Wild *L. aridorum* were less likely to be near nonnative trees than introduced *L. aridorum* (Table 5). Introduced *L. aridorum* were near the shrub *S. tenax* more often than were wild *L. aridorum* and were near shrubby *Quercus* spp. more often than were random locations (Table 5). Introduced *L. aridorum*

Table 4 Means (\pm SEM) for (A) soil characteristics and (B) vegetative characteristics that differed between sites and locations supporting *L. aridorum*

	Wild locations					Introduced locations					Random locations					Statistical significance
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 3	Site 4	Site 5	Site 3	Site 4	Site 5	Site 3	Site 4	Site 5		
(A) Soil characteristics																
Copper ($\mu\text{g}/\text{cm}^3$)	1.7 (0.3)bc	1.6 (0.1)bc	2.6 (0.5)b	0.8 (0.2)c	2.9 (0.2)b	8.0 (1.1)a	0.8 (0.2)c	2.9 (0.2)b	8.1 (1.0)a	1.5 (0.3)bc	NA	8.1 (1.0)a	1.5 (0.3)bc	NA	$F = 21.9$, $df = 3$, $P < 0.001$	
Iron ($\mu\text{g}/\text{cm}^3$)	22 (3)d	19 (6)d	81 (26)bc	26 (4)cd	128 (35)ab	222 (44)a	26 (4)cd	128 (35)ab	236 (48)a	135 (101)bc	NA	236 (48)a	135 (101)bc	NA	$F = 3.5$, $df = 3$, $P = 0.03$	
Magnesium (meq/ 100 cm^3)	0.06 (0)d	0.1 (0)bcd	0.2 (0.1)ab	0.2 (0.1)a	0.2 (0.1)a	0.08 (0)cd	0.2 (0.1)a	0.2 (0.1)a	0.1 (0)cd	0.15 (0)abc	NA	0.1 (0)cd	0.15 (0)abc	NA	$F = 3.6$, $df = 3$, $P = 0.03$	
Organic matter (%)	0.3 (0.1)c	0.4 (0.1)bc	1.3 (0.2)a	0.6 (0.1)b	1.3 (0.1)a	0.4 (0)bc	0.6 (0.1)b	1.3 (0.1)a	0.4 (0)bc	1.0 (0.2)a	NA	0.4 (0)bc	1.0 (0.2)a	NA	$F = 20.3$, $df = 3$, $P < 0.001$	
pH	4.1 (0.1)e	5.1 (0.2)a	4.1 (0)de	4.4 (0)bcd	4.7 (0.1)b	4.6 (0.1)bc	4.4 (0)bcd	4.7 (0.1)b	4.3 (0.5)cde	4.3 (0.1)cde	NA	4.3 (0.5)cde	4.3 (0.1)cde	NA	$F = 3.3$, $df = 3$, $P = 0.04$	
Phosphorus ($\mu\text{g}/\text{cm}^3$)	2.3 (0.7)cd	4.3 (2)bcd	12.0 (4)bc	1.8 (0)d	13.3 (2)b	32.0 (6)a	1.8 (0)d	13.3 (2)b	23.8 (5)a	5.3 (2)bcd	NA	23.8 (5)a	5.3 (2)bcd	NA	$F = 6.1$, $df = 3$, $P = 0.003$	
Sulfur ($\mu\text{g}/\text{cm}^3$)	19 (0.5)bcd	21 (0.7)a	20 (0.3)ab	17 (2)d	20 (0)abc	19 (0.3)d	17 (2)d	20 (0)abc	19 (0.6)cd	20 (0.3)abcd	NA	19 (0.6)cd	20 (0.3)abcd	NA	$F = 4.0$, $df = 3$, $P = 0.02$	
(B) Vegetative characteristics																
Overstory distance (cm)	507 (63)b	983 (132)a	131 (27)c	243 (40)c	514 (80)b	1,105 (83)a	243 (40)c	514 (80)b	790 (184)b	184 (40)c	503 (84)b	790 (184)b	184 (40)c	503 (84)b	$F = 14.4$, $df = 4$, $P < 0.001$	
Shrub distance (cm)	309 (72)c	114 (28)d	161 (27)cd	147 (29)cd	636 (79)b	1,289 (74)a	147 (29)cd	636 (79)b	708 (128)b	141 (29)d	591 (70)b	708 (128)b	141 (29)d	591 (70)b	$F = 23.0$, $df = 4$, $P < 0.001$	
Canopy density (%)	6.0 (4)bc	1.0 (1.0)c	18.3 (5)a	6.6 (3)b	14.7 (3)a	0.7 (1)c	6.6 (3)b	14.7 (3)a	21.3 (9)b	6.9 (2)b	22.1 (5)a	21.3 (9)b	6.9 (2)b	22.1 (5)a	$F = 7.1$, $df = 4$, $P < 0.001$	
Number of woody stems	1.6 (0.4)bc	0.9 (0.4)d	1.1 (0.3)cd	4.4 (1.8)ab	0.1 (0.1)e	0 (0)e	4.4 (1.8)ab	0.1 (0.1)e	1.1 (0.6)de	13.3 (3.6)a	0 (0)e	1.1 (0.6)de	13.3 (3.6)a	0 (0)e	$F = 3.8$, $df = 4$, $P = 0.006$	
Bare ground (%)	62 (6)abc	58 (7)bcd	67 (5)ab	49 (7)cde	60 (6)bcd	78 (4)a	49 (7)cde	60 (6)bcd	42 (7)de	37 (7)e	46 (8)cde	42 (7)de	37 (7)e	46 (8)cde	$F = 4.9$, $df = 4$, $P = 0.001$	
Leaf litter (%)	8 (5)bc	13 (5)ab	18 (5)a	12 (3)a	12 (3)ab	2 (1)c	12 (3)a	12 (3)ab	16 (6)ab	18 (5)a	27 (8)a	16 (6)ab	18 (5)a	27 (8)a	$F = 3.8$, $df = 4$, $P = 0.006$	

Means with different letters within a row are significantly different

Table 5 Relative frequency (\pm SEM) that shrub and tree species were nearest to, and ground cover species were most abundant at, locations of wild and introduced *Lupinus aridorum* and random locations across five sites in central Florida, USA. Relative frequency (\pm SEM across four sites) that six categories of detritus were present at locations of wild and introduced *L. aridorum* and random locations. Introduced locations are significantly different from wild locations in type of nearest tree, shrub, abundant ground cover, and detrital category and also significantly different than random locations in nearest shrub and abundant ground cover

Locations	Tree species					
	<i>Persea borbonia</i>	<i>Pinus</i> spp.	<i>Quercus</i> spp.	Other native spp.	Other nonnative spp.	
Introduced	18.3 (18.3)	29.2 (29.2)	34.2 (10.8)	5.0 (5.0)	13.3 (13.3)	
Wild	28.3 (11.7)	43.3 (3.3)	25.0 (19.5)	3.3 (1.7)	0.0 (0.0)	
Random	10.0 (10.0)	25.0 (22.5)	41.7 (11.7)	10.0 (2.9)	13.3 (13.3)	
	Shrub species					
	<i>Serenoa repens</i>	<i>Sideroxylon tenax</i>	<i>Quercus</i> spp.	Other spp.		
Introduced	27.5 (7.5)	17.9 (10.1)	22.1 (4.8)	32.5 (11.8)		
Wild	21.7 (14.8)	3.3 (1.7)	23.3 (18.3)	51.7 (20.5)		
Random	32.6 (9.0)	15.4 (10.3)	8.3 (8.3)	43.7 (12.3)		
	Ground cover plants					
	<i>Cladonia leporina</i>	Grass spp.	<i>Paronychia chartacea</i> spp. <i>chartacea</i>	Other native spp.	Other nonnative spp.	
Introduced	0.0 (0.0)	8.8 (3.1)	24.2 (19.4)	53.8 (12.6)	13.3 (8.8)	
Wild	28.3 (17.4)	11.7 (6.0)	1.7 (1.7)	55.0 (8.6)	3.3 (3.3)	
Random	1.7 (1.7)	20.0 (5.0)	6.7 (4.4)	58.3 (4.4)	13.3 (7.3)	
	Detritus					
	No detritus	Leaves of herbs	Leaves of broadleaf woody plants	Pine needles	Twigs/branches	Mixture of detritus
Introduced	28.8 (26.3)	5.0 (5.0)	13.3 (10.9)	2.1 (2.1)	2.1 (2.1)	48.8 (22.0)
Wild	15.0 (0.0)	10.0 (2.9)	10.0 (5.7)	6.7 (6.7)	6.7 (6.7)	51.7 (7.3)
Random	22.5 (13.7)	10.3 (5.1)	15.2 (10.3)	5.3 (5.3)	1.7 (1.7)	48.5 (20.3)

were near the ground cover plant *P. chartacea* ssp. *chartacea* more often and *C. leporina* less often than were wild *L. aridorum* (Table 5). The ground cover near introduced and random locations also differed: grass was less abundant at introduced locations (Table 5). Lastly, introduced *L. aridorum* and random locations were more likely to have no detritus within 2 m² than wild *L. aridorum* (Table 5).

Discussion

How does microhabitat at locations supporting wild *L. aridorum* vary from random locations within Florida scrub?

Many characteristics of the microhabitat were similar between locations of wild *L. aridorum* and random locations. The lack of strong fit of our AIC_c models to the data indicates that we failed to capture all the variation in microhabitats. However, wild *L. aridorum* tended to grow in areas closer to trees and shrubs, with lower soil moisture, and with a greater mixture of detritus than what we would randomly expect. The preference of *L. aridorum* for well-drained soils is a common life history trait of gap specialists (Richardson et al. 2013), but the association with trees, shrubs, and detritus was unexpected given that gap specialists usually have a negative association with these habitat characteristics (Quintana-Ascencio and Morales-Hernandez 1997; Menges et al. 1999; Peterson et al. 2013; Richardson et al. 2013). Ecological research often focuses on competition between plant species, but plant species may facilitate the growth and survival of other species, particularly in environments with dry soils and high temperatures (Flores and Jurado 2003; Padilla and Pugnairé 2006). *L. aridorum* rarely was directly beneath a tree or shrub, but was often close enough to be partially shaded by these taller plants. Additionally, our results indicate that *L. aridorum* may be associated with particular tree and shrub species, such the tree *P. borbonia* and the shrub *S. repens*, because it grew in proximity to these plant species more often than would be randomly expected.

How does microhabitat differ between locations with wild or introduced populations?

Some microhabitat characteristics at locations where *L. aridorum* were introduced were similar to

microhabitat supporting wild *L. aridorum*, but the overall plant community in the under, mid, and overstory was different, as were soil characteristics and detritus. The plant community near introduced plants contained more nonnative plant species than the plant community near wild plants. The microhabitat characteristics near introduced plants were more similar in most ways to random locations than wild locations, such as the composition of the plant community in the overstory, soil characteristics, and the detrital layer. This similarity could be due to the fact that introduced and random locations were sampled within the same sites and two-thirds of the wild locations were sampled primarily from different sites (i.e., more variation in microhabitat between sites than within sites).

The microhabitat characteristics associated with introduced plants may also largely be a result of how and where they were planted within sites. Introduced sites were either already very open in the under, mid, and overstory and free of detritus at the time of planting or the sites were mechanically cleared before planting. Natural sites have more canopy cover and detritus than introduced sites largely due to the suppression of fire. Introduced plants may not differ in many ways from random locations because the microhabitat preferences for this species were unknown at the time of planting, so individual plants may have been randomly placed within the sites. The planting regime, coupled with a wider tolerance to environmental conditions than previously assumed, may explain why introduced plants are in microhabitat that differs from microhabitat of wild plants. Regardless of why microhabitat of introduced plants is similar to random locations, the fact is that these plants have survived and produced recruits in a broader niche than where wild plants are found. However, this study can only document short-term survival in this broader niche because these new populations have only existed for a maximum of 5 years. We are collecting demographic data yearly so we can estimate the long-term extinction risk of these new populations (unpublished data).

Conclusion

Lupinus aridorum is a diploid understory plant in Florida scrub, and whereas most plants studied to date

in this habitat often responded negatively to canopy and litter cover (e.g., Quintana-Ascencio and Morales-Hernandez 1997; Menges et al. 2006), *L. aridorum* appears to be an exception and can grow in association with some canopy and litter cover. Future research should investigate the possible role of facilitation on growth and survival of *L. aridorum* and other short-lived perennial plants in Florida scrub because facilitation has rarely been reported in this habitat (except see Mondo et al. 2010). Additionally, we have narrowed the list of microhabitat characteristics that may influence the distribution of *L. aridorum* and future research should elucidate the relative impact of these characteristics on the fitness and population dynamics of *L. aridorum*.

Future research also should explore whether wild populations of *L. aridorum* are seed-limited because our results from introduced populations indicate that the realized niche is narrower than the fundamental niche. Seed-limited populations have fewer individuals than the habitat can support because too few seeds are produced or because the seeds that are produced fail to reach potential recruitment sites (Eriksson and Ehrlén 1992; Svenning and Wright 2005). If wild populations of *L. aridorum* are seed limited and do indeed have a wider fundamental niche than currently realized, then one possible strategy to increase population size might be to introduce seeds and seedlings into acceptable unoccupied microhabitat.

Our study cannot determine mechanisms that influence the spatial distribution of *L. aridorum*. Field assays with *L. aridorum* are needed to examine the extent to which recruitment into populations is limited by seed dispersal or habitat, followed by studies to examine the specific mechanisms that cause seed or habitat limitation. Populations of plants are often limited by seed and habitat (e.g., Orrock et al. 2006; Dybzinski and Tilman 2012) and the limiting mechanisms need to be identified to conserve rare plant species.

In conclusion, our results will inform additional experiments on in situ conservation and reintroduction of *L. aridorum* as well as related species in Florida. Over 300 species within the Fabaceae, including additional *Lupinus* species, grow in Florida and our results may be used to guide their conservation if they occupy a similar niche. Our results also may be applicable to other short-lived perennial species in arid environments because these species are narrowly

adapted to the disturbance regime and microhabitat specific to these harsh environments (Hartnett and Richardson 1989; Menges et al. 1999; Richardson et al. 2013). Ultimately, by learning about the microhabitat of an endangered plant species, appropriate management programs to conserve and restore populations of the endangered species and its microhabitat can be designed.

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