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Cover Page Footnote

In Monaco, T.A. et al. comps. 2011. Proceedings – Threats to Shrubland Ecosystem Integrity; 2010 May 18-20; Logan, UT. Natural Resources and Environmental Issues, Volume XVII. S.J. and Jessie E. Quinney Natural Resources Research Library, Logan Utah, USA.

Bottom-up Effects of Substrate on Two Adjacent Shrub Communities and the Distribution of a Rare and Endangered Plant Species, *Astragalus jaegerianus* Munz.

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ABSTRACT

*Edaphic habitats are botanically interesting because of differences in vegetation with neighboring sites and because they tend to harbor rare species. In the central Mojave Desert, there are granite colluvial substrates where creosote bush, the dominant shrub in the area, is sparser and generally smaller than in the neighboring creosote bush communities. It is on these sites that the Lane Mountain milkvetch, a rare and federally endangered species, is restricted. The milkvetch is a nitrogen-fixer and grows under and within the canopy of host shrubs. Our previous studies have demonstrated that the milkvetch has no preference for species of host shrub, except *Larrea tridentata*, which appears to be an unsuitable host plant for the milkvetch. In this study, we surveyed three transects within milkvetch habitats and three transects in adjacent creosote bush habitats in the year 2000 and again in 2010, a period coincident with long-term drought conditions in the Mojave Desert. Our results show that adjacent milkvetch and creosote bush shrub communities differ significantly in shrub height, shrub volume, and shrub density in the year 2000: the shrubs in milkvetch communities were more numerous but smaller compared to adjacent creosote bush scrub. Species richness also differed between communities in the year 2000: milkvetch communities contained 19 different shrub species and creosote bush communities had only 9 species. Surveys in 2010 show that the drought had significant negative effects on both shrub communities. Total shrub mortality (166 shrubs) was high compared to shrub recruitment (16 shrubs), and the majority of mortality and recruitment occurred in milkvetch communities (131 deaths and 16 recruits). Shrub densities decreased significantly in milkvetch communities in 2010, but were still considerably higher than in creosote bush communities. These results suggest that the restricted distribution of the Lane Mountain milkvetch may be the result of higher shrub densities in milkvetch shrub communities; increased shrub densities increases the proximity of suitable host shrubs, which in turn increase the probability of successful seed dispersal and establishment.*

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INTRODUCTION

Ecosystems often contain dominant plant communities composed of species that attain high densities within the prevailing edaphic and climatic conditions associated with that ecosystem. Within these dominant plant communities, abrupt changes in soil characteristics can create islands of distinctive vegetation in which the regionally dominant vegetation is excluded or modified (Kruckeberg and Rabinowitz 1985; Mason 1946). These anomalous habitats may be geographically isolated and of limited areal extent, and they are usually less productive than the surrounding, regionally dominant vegetation (Meyer 1986; Whittaker 1954). These anomalous edaphic communities are botanically interesting

because they demonstrate the bottom-up effect of soils on plant communities, and because they tend to harbor unusual species that may be rare and endemic, or represent major disjunct populations (Kruckeberg and Rabinowitz 1985; Gankin and Major 1964; Whittaker 1954).

The soil properties responsible for vegetation differences within edaphic communities may include the presence of elements toxic to the physiology of most plants (for example, magnesium in serpentine soils (Proctor 1970), or calcium and aluminum in limestone soils (Lee 1999)). Vegetation differences may be due to soil deficiency in iron or calcium (Brady and others 2005; Lee 1999), or deficiency in the essential nutrients nitrogen, potassium, and

phosphorous (Zohlen and Tyler 2004; Proctor and Woodell 1975). Vegetation differences in edaphic communities may also be due to deficiencies in soil moisture (Ware 1991; Baskin and others 1972). In some cases the soil properties responsible for vegetation differences in edaphic communities are complicated and not fully understood (for example, gypsum plants; Palacio and others 2007; Meyer 1986). Some edaphic communities may serve as refugia for plants that can tolerate toxic compounds (in other words, the refugia hypothesis, Gankin and Major 1964), while other edaphic communities may contain some feature essential for an edaphic species (in other words, the specialist hypothesis, Meyer 1986).



(a)



(b)

Figure 1. Adjacent plant communities at Gemini Conservation Area in January 2010, Fort Irwin, CA (elevation 1110 m). A. Creosote bush-dominated community with elements of Joshua Tree woodlands including *Yucca brevifolia* (tree in the left middle-distance). The abundant, large, dark shrubs are creosote bush (*Larrea tridentata*). B. Milkvetch granite barren, with its characteristic high density of small shrubs in which creosote bush is absent or reduced. The dark shrub in the right-foreground is a lone creosote bush.

Astragalus jaegerianus Munz (Fabaceae), the Lane Mountain milkvetch, is a narrowly endemic, herbaceous perennial restricted to rocky granite outcrops (barrens) in the central Mojave Desert. These granite barrens occur at an elevation between 900 and 1200 m, and are easily recognized by their reduced vegetation compared to the adjacent dominant vegetation of the area, creosote bush scrub, a shrub community dominated by *Larrea tridentata* (D.C.) Cov. (creosote bush) with common associates including *Ambrosia dumosa* (A. Gray) W. W. Payne (burro-weed), *Krameria erecta* Schult. (pima rhatany), *Ephedra nevadensis* S. Wats. (Nevada ephedra), and *Grayia spinosa* (Hook.) Moq. (spiny hopsage), as well as the *Yucca brevifolia* Engelm. (Joshua tree). *Larrea tridentata*, which is dominant in the adjacent vegetation (figure 1A), is conspicuously absent or much reduced within the shrub community on granite barrens (figure 1B). Similarly, *A. jaegerianus* does not occur outside of granite barrens in adjacent creosote bush scrub. The shrub community is important to *A. jaegerianus*, a climbing herbaceous perennial, because it uses shrubs as host plants (Gibson and others 1998, Huggins and others 2010). *Astragalus jaegerianus* completes its entire lifecycle within its host shrub; it germinates or resprouts under the shrub canopy in winter, then climbs through the interior of the shrub emerging onto the canopy where it flowers and sets fruits in late spring. *Astragalus jaegerianus* then goes dormant through the summer until it resprouts again with winter rains.

The central purpose of this study is to investigate the factors that act to restrict *A. jaegerianus* to granite barrens of the central Mojave Desert. To explore this phenomenon we (1) describe the edaphics and vegetation of shrub communities on granite barrens and adjacent creosote bush scrub, (2) analyze *A. jaegerianus*' host shrub preferences, and (3) propose a hypothesis explaining the restricted distribution of *Astragalus jaegerianus* on granite barrens as a function of shrub density and size. In addition, we (4) describe how recent drought conditions in the central Mojave have affected *A. jaegerianus* and the shrub in granite barrens and creosote bush scrub communities. Severe drought conditions in the Mojave began in 1999 and are predicted to continue for decades (Hereford and others 2006), or may

continue indefinitely under warmer temperature conditions projected by global climate change-type drought (Cook and others 2004; Breshears and others 2005; Seager and others 2007). These recent drought conditions have led to unusually high shrub mortality and canopy dieback in the Mojave Desert and other parts of the arid southwest US (Bowers 2005; Miriti and others 2007; Hamerlync and McAuliffe 2008; Hamerlync and Huxman 2009).

METHODS

Study Site

Astragalus jaegerianus exists in small fragmented populations within an area of less than 240 km². Roughly two-thirds of all known *A. jaegerianus* populations occur within the boundaries of the US Army's National Training Center at Fort Irwin, approximately 50 km NE of Barstow, California (Charis 2002). The *A. jaegerianus* populations described in this study occurred within Brinkman Wash and the Gemini Conservation area (previously Goldstone), one of four locations previously established as discrete areas of *A. jaegerianus* distribution (Charis 2002; Walker and Metcalf 2008). The soils at these sites are composed of shallow granitic colluvium on rocky, granitic outcrops, within the transition zone between Mojavean creosote bush scrub and Joshua tree woodland communities (sensu. Thorne 1982). Adjacent creosote bush communities occur on deeper (greater than 1 m) granite alluvium substrates.

Vegetation

In 1999, five 1-ha plots on granite barrens within the Brinkman Wash area were systematically searched for *A. jaegerianus*. The shrub communities within these plots were visually similar to other shrub communities supporting *A. jaegerianus* across its range. Shrubs harboring *A. jaegerianus* were marked and their UTM coordinates recorded using GPS. The species identity of these host shrubs was also noted to determine *A. jaegerianus* host preferences. Shrub density, cover, and volume within the five granite barren plots were sampled using four belt-transects per plot (Mueller-Dombois and Ellenberg 1974). For

each of these belt-transects in granite barrens, four additional belt-transects were sampled in near-by or adjacent creosote bush scrub, in order to compare both shrub communities. The belt-transects were 24 m long, and either 2 m wide for sampling small shrubs, or 4 m wide for sampling *Larrea tridentata* and *Yucca brevifolia*. The belt-transects were permanently marked using iron rebar stakes and UTM coordinates were recorded. Density was determined by tallying all shrubs in the belt-transect, and cover and volume was determined for all small shrubs in the first 12 m of the belt-transect and for all *L. tridentata* and *Y. brevifolia* for the total length of the belt-transect. Cover was calculated using the formula for an ellipse (ellipse area = $\pi d_1 d_2 / 4$ where d_1 = maximum shrub diameter and d_2 = diameter perpendicular to the maximum diameter), and volume for an ellipsoid (volume = area*h/2, where h = height of shrub). In 2010, three of the five granite barren plots and their associated creosote bush scrub transects were re-sampled to determine the response of each shrub community to the drought conditions which began in 1999.

In addition to the five study sites described above, two more 1 ha study plots were established in 2003 in the Gemini Conservation Area approximately 6 km north of Brinkman Wash study plots. These Gemini study plots were intended for long-term monitoring of *A. jaegerianus* populations, and together with two of the Brinkman Wash study plots established in 1999 were surveyed annually starting in 2003. Like the Brinkman Wash study plots, each shrub within the 1-ha Gemini study plots was systematically search for *A. jaegerianus*, and shrubs harboring *A. jaegerianus* were marked, their UTM coordinates recorded, and the identity of host shrubs was noted. The Gemini study plots were not part of the Brinkman Wash shrub vegetation study, and so contained no belt transects.

Host Shrubs

Astragalus jaegerianus uses various shrub species as hosts (table 1). To determine whether these different values for host shrubs represent preferences or merely reflect the relative abundances of shrub species on granite barrens, a total of the observed species used by *A. jaegerianus* within all five 1 ha plots was compared to an expected value based on

shrub relative densities calculated from the belt transects. The expected values (expected value = relative density of each shrub species × number of shrubs with *A. jaegerianus* at the site sampled) were calculated for each shrub species in each of the five study sites, and the expected values for each species for each study site were summed. A goodness of fit analysis (Zar 1974) was performed to determine if observed values for a host were statistically different from expected values. Many of the expected values for the less common shrub species had to be combined together in “other species” to meet the recommendations of Cochran (1954): no expected frequency should be less than 1.0 and no more than 20 percent of the expected frequencies should be less than 5.0. Because the initial goodness of fit analysis had a significant chi-square value, subdivisions of the goodness of fit analysis (Zar 1974) were performed on subdivided data sets. *Larrea tridentata* had a very large partial chi-square value, so a goodness of fit was performed on the data set “*L. tridentata* versus all

other shrubs” and another analysis on the data set of shrubs excluding *L. tridentata*.

Edaphic Analysis

Soil pits were dug at milkvetch sites and at a neighboring creosote bush scrub site. Pits were dug to the bedrock at milkvetch granite barren sites (5 to 40 cm) and at the creosote bush scrub sites to ca. 80 cm deep. The soil depth to impervious layers (if any) was noted. Each soil sample was placed in a re-sealable plastic bag and brought back to UCLA where they were immediately air dried. Samples were then gently pulverized to break up aggregates and then sieved to remove particles > 2 mm. The samples were analyzed by the Agriculture and Natural Resources Analytical Laboratory at the University of California at Davis for particle size distribution (sand, silt, and clay), organic content, pH, salts (Ca, Mg, Na, electrical conductivity), nutrients [N (N_{TKN}), NH_4-N , NO_3-N], P, K], selenium, iron, and cation exchange capacity.

Table 1. The change in abundance of host shrubs with live *A. jaegerianus* at Brinkman Wash (1999-2010) and the Gemini Conservation Area (2003-2010). *Astragalus jaegerianus* may survive after its host shrub has died (dead shrub), and is rarely found growing without a host shrub (no host). *Astragalus jaegerianus* was not found growing within *Larrea tridentata*. Brinkman Wash was first surveyed in 1999, and the Gemini Conservation Area in 2003.

Brinkman Wash			Gemini Conservation Area		
Host	1999	2010	Host	2003	2010
<i>Eriogonum fasciculatum</i>	21	2	<i>Eriogonum fasciculatum</i>	20	1
<i>Thamnosma montana</i>	18	4	<i>Thamnosma montana</i>	6	1
dead shrub	16	1	<i>Ericameria cooperi</i>	6	0
<i>Ephedra nevadensis</i>	15	1	<i>Ambrosia dumosa</i>	3	3
<i>Salazaria mexicana</i>	8	1	<i>Ephedra nevadensis</i>	2	2
<i>Ericameria teretifolia</i>	7	2	<i>Ambrosia salsola</i>	2	0
<i>Ericameria cooperi</i>	6	0	<i>Encelia actonii</i>	2	0
<i>Ambrosia dumosa</i>	6	1	<i>Xylorhiza tortifolia</i>	1	0
<i>Xylorhiza tortifolia</i>	5	0	<i>Krameria erecta</i>	1	0
<i>Ambrosia salsola</i>	4	1	<i>Ericameria teretifolia</i>	0	0
no host	2	0	<i>Salazaria mexicana</i>	0	0
<i>Krameria erecta</i>	1	0	dead shrub	0	0
<i>Encelia actonii</i>	0	0	no host	0	0
<i>Larrea tridentata</i>	0	0	<i>Larrea tridentata</i>	0	0
Total	109	13	Total	43	7

RESULTS

Edaphics

The pooled results of the edaphic analysis are presented in table 2. Differences in the origin of soils within granite barrens and creosote bush-dominant communities result in soils of different depths. Soils within granite barrens are a product of granite decomposition within the granite barrens themselves (colluvial). Consequently, soils within granite barrens are shallow, with parent granite no deeper than 40 cm from the soil surface, but commonly shallower, with exposed granite visible on low alternating ridges within the granite barrens (figure 2). Soils within adjacent creosote bush scrub are composed of alluvium from the surrounding hills including the low ridges within the milkvetch granite barrens.

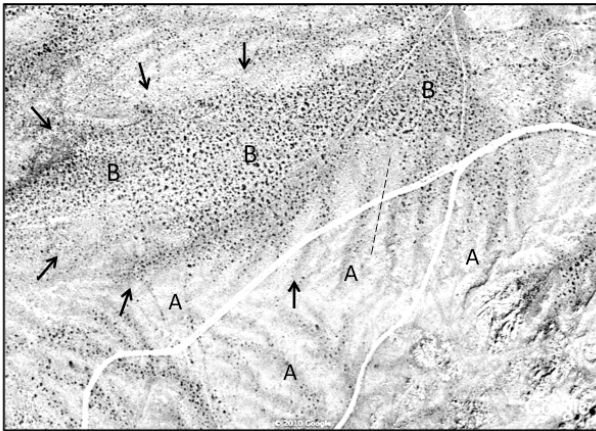


Figure 2. A Google Earth satellite image of typical milkvetch-granite barrens (A) with adjacent creosote bush scrub (B) at the Gemini Conservation Area (elev. 1110 m) within the National Training Center at Fort Irwin, CA. Creosote bushes are clearly visible as dark spots on deep alluvial soils that support creosote bush scrub (B). Visible within the milkvetch barrens (A) are the exposed granite ridges typical of milkvetch habitat (- - -) where creosote bush is absent or reduced in size and density. Soil depths in milkvetch granite barrens may reach 30 cm in drainages between ridges. Arrows indicate the direction of run-off from elevated milkvetch granite barrens into lower areas where alluvium accumulates producing deep soils (>1 m) that support creosote bush scrub.

Consequently, soils with creosote bush scrub are deep, typically greater than 1 m in depth. Some physical and chemical properties of the soil of milkvetch granite barrens and adjacent creosote bush scrub are presented in table 2. Soil textures within the creosote bush scrub and milkvetch granite barrens

are similar and typical of Mojave Desert soils composed primarily of sand (Stevenson and others 2009; Young and others 2009). Electrical conductivity, CaCO_3 , and pH are more or less similar between communities, and within the range of typical Mojave Desert soils but at the low end of the range (Graham and O'Geen 2010; Cox and others 1984, Romney and others 1973). Both nitrogen (total Kjeldahl N and total available N ($\text{NH}_4\text{-N}$ plus $\text{NO}_3\text{-N}$)), phosphorous and potassium are somewhat lower in granite barrens than in adjacent creosote bush scrub communities (table 2), but both communities have values higher than other Mojave Deserts creosote bush sites (Schlesinger and others 1996), and within the range of typical Mojave Desert soils (Schlesinger and others 1996; Romney and others 1973; Cox and others 1984; Rundel and Gibson 1996). Like NPK, elements such as calcium (Ca), sodium (Na), and selenium (Se) are somewhat higher in the alluvial creosote bush sites. These higher levels are likely to be the result of the accumulation and concentration of particles dissolved in run-off from the higher elevations surrounding creosote bush scrub sites. The slightly higher organic content in creosote bush scrub may account for slightly higher nitrogen in creosote bush scrub soils. In both communities, iron (Fe) occurs at levels higher than reported in other Mojave Desert soils (0 to 2.0 ppm reported in Romney and others 1973 for soils of the Nevada Test Site), and occurs at higher levels in milkvetch granite barrens (4.0 ppm Fe) than in creosote bush scrub (2.3 ppm, table 2), but both values are well below concentrations that are typically toxic to plants (> 365 ppm, Foy and others 1978).

Host Plants

The chi-square test for goodness of fit for all shrubs (table 3) demonstrates that the observed species spectrum of host shrub frequencies does not fit expected frequencies based on our belt transect data (chi-square = 20.68; critical value = 7.81). One species alone, *Larrea tridentata*, constitutes over 57 percent of the chi-square value, and is significantly under-represented as an *A. jaegerianus* host plant (chi-square = 11.98; critical value = 3.84). This result suggests that *Larrea* may be an unsuitable host shrub for *A. jaegerianus*. This unsuitability may be due to *Larrea's* architecture, which is significantly taller than suitable host shrubs, and too tall and open to allow *A. jaegerianus* to climb through and reach its canopy.

Table 2. Physical and chemical properties of substrate at milkvetch granite barrens and creosote bush scrub sites at Brinkman Wash, 2001. Twenty-six soil samples were collected per site. Samples were collected under and between shrub canopies, at a depth of 5 to 40 cm. Values are means (SE).

Substrate Characteristics	Sites	
	Milkvetch Granite Barrens	Creosote Bush Scrub
General Properties		
	colluvium, decomposed granite	alluvium, some sites derived 1° from granite, other sites a mixture derived from granite and sedimentary rock
Physical Properties		
Depth	shallow - parent rock within 40 cm of surface	deep - hard pan deeper than 100 cm of surface
Texture		
Sand %	77 (0.9)	75 (1.3)
Slit %	15 (0.8)	18 (0.9)
Clay %	9 (0.4)	7 (0.6)
Chemical Properties		
Organic content (%)	0.5 (0.06)	0.8 (0.1)
pH	7.4 (0.1)	7.7 (0.1)
Electrical conductivity	0.35 (0.04)	0.86 (0.2)
Ca (meq/L)	2.5 (0.4)	6.9 (1.3)
CaCO ₃ (%)	0.58 (0.2)	0.54 (0.1)
Mg (meq/L)	0.68 (0.1)	0.93 (0.2)
Na (meq/L)	0.31 (0.03)	0.50 (0.07)
Se (ppb)	43.2 (5.2)	144.2 (19.3)
Fe (ppm)	4.0 (0.5)	2.3 (0.19)
Cation exchange capacity	17.0 (0.7)	17.9 (0.8)
N _(Total Kjeldahl N) (%)	0.038 (0.01)	0.060 (0.01)
K (ppm)	11.3 (3.3)	45.0 (10.8)
P (ppm)	9.8 (1.4)	16.2 (2.1)
NH ₄ -N (ppm)	2.2 (0.6)	1.8 (0.3)
NO ₃ -N (ppm)	4.4 (0.9)	15.8 (4.5)
N _(available) (ppm)	6.6 (1.5)	17.6 (4.8)

Excluding *Larrea*, a second, goodness-of-fit test with the remaining shrubs is not significantly different from expected (chi-square = 9.99; critical value = 11.07). Thus, *Eriogonum fasciculatum* Benth. var. *polifolium* (Benth.) Torr. & A. Gray (Mojave buckwheat), *Ericameria cooper* (A. Gray) H. M. Hall (Cooper's goldenbush), *Ephedra nevadensis*, *Ambrosia dumosa*, and *Krameria erecta* are used as host plants in what would be expected from their abundances on the sites. The category "other shrubs," which includes *Encelia actonii* Elmer (Acton's encelia), *Salazaria mexicana* Torr. (Mexican bladder sage), *Ericameria teretifolia* (Durand & Hilg.) Jeps. (green rabbitbrush), *Ambrosia salsola* (Torr. & A. Gray) Strother & B.G.

Baldwin (cheesebush), *Thamnosma montana* Torr. & Frem. (turpentine broom), and *Xylorhiza tortifolia* (Torr. & Gray) Greene (Mojave woody aster), were also used as hosts in the same frequency their abundance would suggest but their sample size is too small to reach any statistically valid result.

Vegetation

As expected from visual differences between communities, shrub characteristics on the granite barrens were very different from adjacent creosote bush scrub (figure 3): shrubs on granite barrens were smaller (0.062 m³ versus 0.86 m³), shorter (27 versus 67 cm), and produced less cover than shrubs in

creosote bush scrub (17 percent versus 25 percent), but were more numerous, resulting in a higher density of shrubs on granite barrens (181 versus 74 shrubs/100 m²). At our study sites, *Larrea* is a taller and larger shrub than *A. jaegerianus* host shrub species (figure 4), and its density is much higher in creosote bush scrub than in milkvetch-granite barrens (figure 5). Since *Larrea* is a large, unsuitable host for *A. jaegerianus* (table 3), its dominance in cover within creosote bush scrub preempts space used by potential host shrubs, further reducing the effective density of host shrubs in creosote bush scrub.

Twenty-five species of perennial shrubs occurred within the belt transects in granite barrens and adjacent creosote bush (figure 6). Transects in both communities supported similar species richness

values; 20 species in granite barrens and 19 species in creosote bush scrub. Of these 25 species, and ignoring the rarer species (< 0.01 percent absolute cover), five species occurred exclusively within granite barren transects, and two species occurred exclusively within creosote bush scrub transects. Three species were common in creosote bush scrub: *Larrea tridentata*, *Ambrosia dumosa*, and *Krameria erecta*, with *Larrea* dominating in absolute (percent) cover. Four species were co-dominants in granite barrens: *Larrea tridentata*, *Eriogonum fasciculatum*, *Ericameria cooperi* and *Ephedra nevadensis*. These four co-dominants, with the exception of *Larrea*, are common *A. jaegerianus* host shrubs, but represent a minute component of the adjacent creosote bush scrub communities.

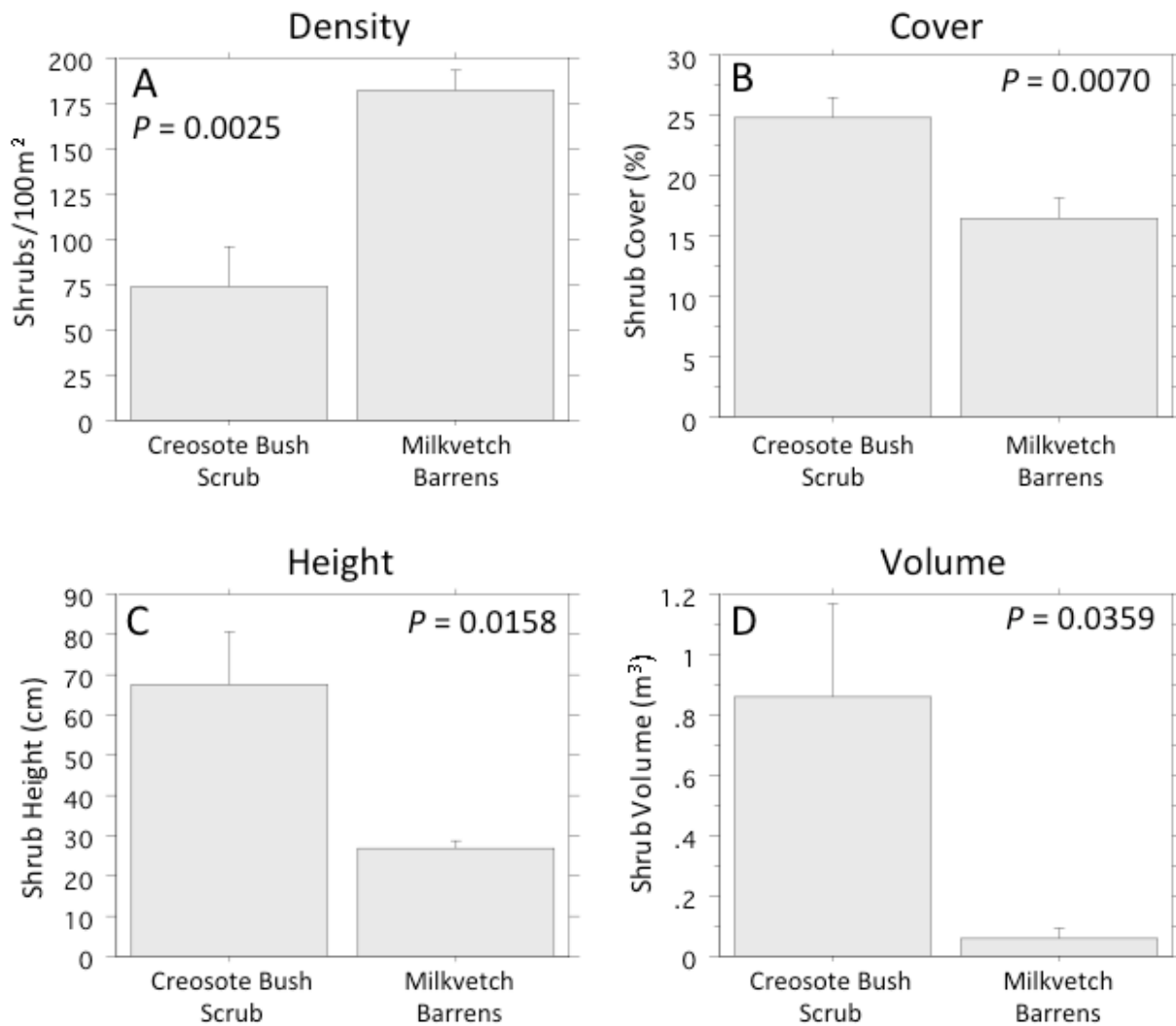


Figure 3. Differences in the distribution and size of shrubs in adjacent shrub communities. Shrubs are significantly larger in creosote bush scrub (C and D) and cover a greater area (B), but shrubs are significantly more numerous in milkvetch granite barrens (A). Bars are means (+ SE).

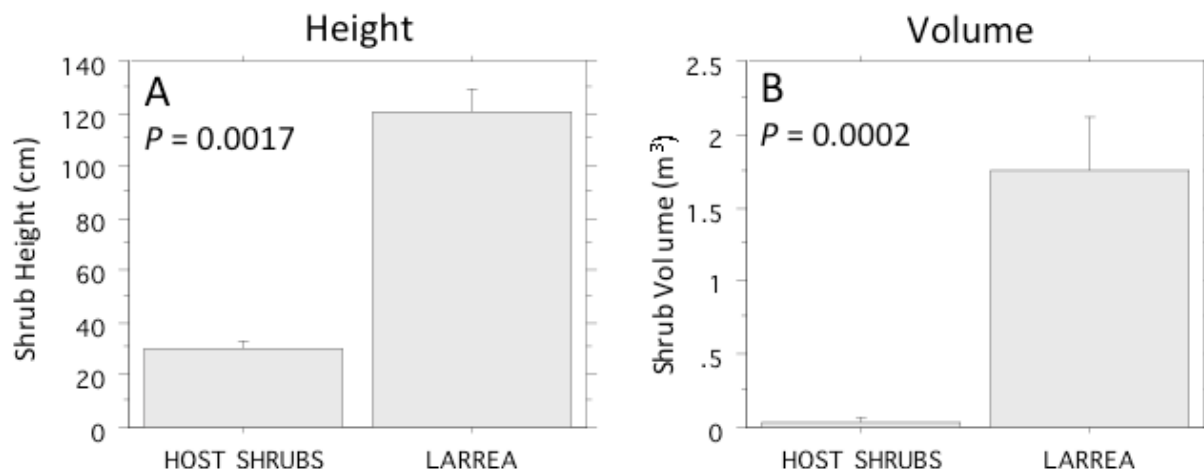


Figure 4. Differences in the size of typical *Astragalus jaegerianus* host shrub species and *Larrea tridentata* (creosote bush), an unsuitable host shrub for *A. jaegerianus*. *Larrea tridentata* shrubs are significantly taller (A) and larger (B) than typical *A. jaegerianus* host shrubs. Bars are means (+ SE).

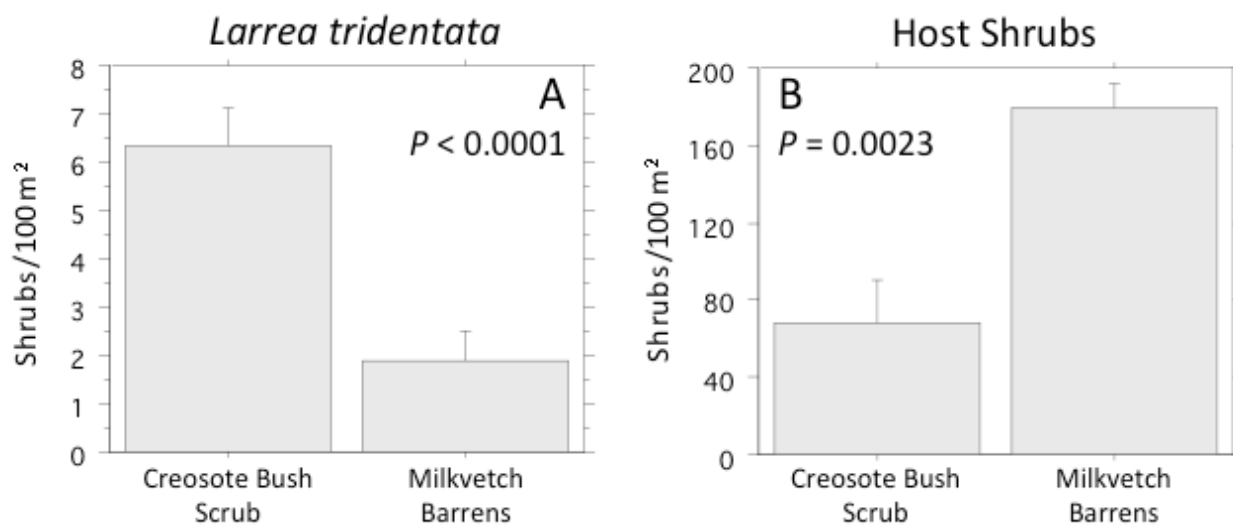


Figure 5. Differences in the distribution of *Larrea tridentata* (A) and potential *Astragalus jaegerianus* host shrubs (B) in creosote bush scrub (CBS) and milkvetch granite barrens (MGB). *Larrea tridentata* is significantly more abundant in CBS than MGB, and potential *A. jaegerianus* host shrubs are significantly more abundant in MGB than CBS. Bars are means (+ SE).

Drought Effects

Three of the five paired sites that we surveyed in 1999 were resurveyed in 2010. The effects of drought on the vegetation structure in the last 10 years are presented in figure 7. Total shrub mortality (166 shrubs) was high compared to shrub recruitment (16 shrubs), and the majority of mortality and recruitment occurred in milkvetch communities (131 deaths and 16 recruits). Values for density and cover were lower in 2010 than in 2000, but the mean shrub density within the granite barrens remained twice as high as pre-drought shrub densities in creosote bush scrub.

Decreases in density represent the death without replacement of shrubs, and decreases in cover represent both death of shrubs and drought pruning of live shrubs. Within shrub transects, shrubs species responded differently to the drought as some species are capable of surviving drought better than others. Within milkvetch barrens, only *Larrea tridentata* maintained the same density over the 10 year period, and the hemi-parasite *Krameria erecta* increased in density. Most species declined 20–50 percent, and *Ericameria cooperi* and *Lycium andersonii* A. Gray, *L. cf. cooperi* A. Gray (Anderson's desert thorn) declined

over 75 percent in density. Species that were little affected by the drought include *Larrea tridentata*, *Thamnosma montana*, *Ephedra nevadensis*, *Salazaria mexicana*. These species maintained 80 percent or more of their measured density in 2000. Within creosote bush scrub sites, *Larrea tridentata* and *Krameria erecta* responded similarly to the drought as they did at the milkvetch barren sites; other species that are found at both sites (*Ambrosia dumosa*, *Ephedra nevadensis*, and *Thamnosma montana*) had slightly greater declines than observed on the milkvetch barrens, and species more-or-less unique to the creosote bush scrub sites (*Lycium andersonii*, *Krascheninnikovia lanata* (Pursh) A. D. J.

Meeuse & Smit) (winterfat) suffered big declines in density.

Astragalus jaegerianus mortality was high during the drought at our long-term study sites: At Brinkman Wash, only 13 of 109 *A. jaegerianus* survived from 1999, and at the Gemini Conservation Area only 7 of 43 *A. jaegerianus* survived from 2003 (table 1). The highest *A. jaegerianus* mortality (19 plants) occurred in *Eriogonum fasciculatum*, the most common host shrub in 1999 and in 2003 with 41 *A. jaegerianus*. By 2010, *Thamnosma montana* Torr. & Frem. was the most common host shrub with 5 *A. jaegerianus*, followed by *Ambrosia dumosa* (4), *Ephedra nevadensis* (3), and *Eriogonum fasciculatum* (3).

A. All shrub species

Species	Observed	Expected	(O-E) ² /E
<i>Eriogonum fasciculatum</i>	22	15.69	2.53
<i>Larrea tridentata</i>	1	13.90	11.97
<i>Ericameria cooperi</i>	7	10.98	1.44
<i>Ephedra nevadensis</i>	15	9.16	3.71
Other species	27	22.25	1.01
	72		20.66 **

B. All shrub species excluding *Larrea tridentata*

Species	Observed	Expected	(O-E) ² /E
<i>Eriogonum fasciculatum</i>	22	18.31	0.74
<i>Ericameria cooperi</i>	7	13.87	3.40
<i>Ephedra nevadensis</i>	15	10.58	1.84
<i>Ambrosia dumosa</i>	6	5.94	0.00
<i>Krameria erecta</i>	1	5.29	3.47
Other species	20	17.01	0.53
	71		9.98

C. *Larrea tridentata* versus all other shrub species

Species	Observed	Expected	(O-E) ² /E
<i>Larrea tridentata</i>	1	13.905	11.977
other species	71	58.095	2.867
	72		14.844 **

Table 3. *Astragalus jaegerianus* host shrub preference using chi-square analysis with (A) creosote bush (*Larrea tridentata*), (B) without creosote bush, and (C) creosote bush versus all other shrubs. Creosote bush is significantly under-represented as a *A. jaegerianus* host shrub, and is probably unsuitable (n = 72 total host shrubs).**** = significant (P = 0.01).

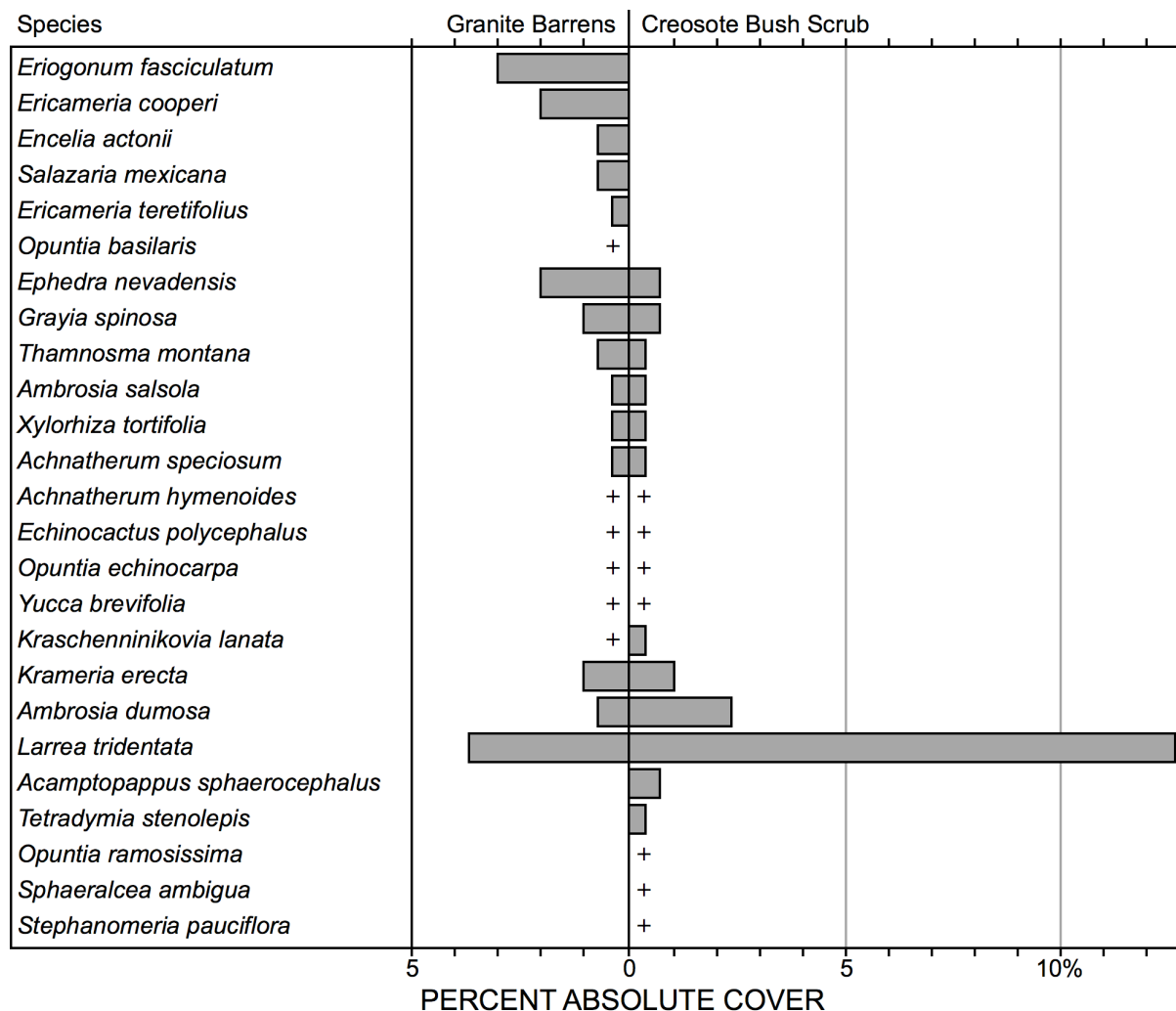


Figure 6. Mean absolute (percent) cover for perennial shrubs occurring within belt transects in granite barrens and adjacent creosote bush-dominated vegetation, at the National Training Center, Fort Irwin, CA (2000). Bars are mean absolute cover of five study sites rounded to the nearest 1/3 percent; "+" = plants with < 0.1 percent cover.

DISCUSSION

Granite barrens of the central Mojave Desert (900 to 1200 m) support shrub communities derived from the dominant, surrounding vegetation of the area, but modified by edaphic circumstances into distinctive communities that harbor the endemic species, *Astragalus jaegerianus*. The vegetation that surrounds the granite barrens is a transition vegetation composed of lower elevation creosote bush scrub (below sea level to 1400 m) with elements of higher elevation Joshua tree woodlands (1055 to 1525 m) (Thorne 1982). The shrub flora of granite barrens is derived entirely from these two plant communities, but the relative abundance, density, and size of shrubs is both visually and statistically

different: the shrub community on granite barrens is composed of smaller shrubs at a significantly higher density than in the surrounding creosote bush dominant community, and three of the most common shrubs on granite barrens, *Eriogonum fasciculatum*, *Ericameria cooperi*, and *Ephedra nevadensis*, are a minor component of the adjacent creosote bush dominant community. The six species found exclusively in granite barren transects (figure 6) are characteristic of a subclass of desert rupicolous scrub described by Thorne (1982) as "mixed desert scrub": an open, edaphically controlled community found on rocky, non-calcareous slopes where soil development is restricted. Mixed desert scrub is one of the most complex and least understood desert plant communities because it varies floristically with

latitude, rainfall, and substrate, and was thought by Thorne to involve more than one community (Thorne 1982). Like mixed desert scrub, the perennial flora of granite barrens lacks clearly dominant species, but displays an impressive variety of desert growth habits including shrubby species (for example, *Eriogonum fasciculatum*, *Ericameria cooperi*, *Ephedra nevadensis*, *Larrea tridentata*), annuals (for example, *Phacelia tanacetifolia* Benth., *Pholistoma auritum* (Lindley) Lilja, *Coryopsis biglowvii* (A. Gray) H. M. Hall) (Bigelow's coreopsis), stem-succulents (*Opuntia*), leaf semi-succulents (*Yucca*), perennial grasses (*Achnathrum speciosum* (Trin. & Rupr.) Barkworth (desert stipa), and herbaceous perennials such as *Astragalus jaegerianus*. As a consequence of (1) the unique properties of the shrub community on granite barrens relative to the surrounding dominant vegetation, (2) the limited geographic distribution of these barrens in the central Mojave Desert, (3) the prominent role of edaphics in controlling community structure, and (4) the presence of the endemic indicator species *Astragalus jaegerianus*, a community level designation "milkvetch barrens" as a distinct sub-community within Thorne's mixed desert scrub is proposed here.

Soil chemistry is unlikely to be the edaphic factor responsible for the stunted vegetation of milkvetch barrens: while some difference in soil chemistry exist between milkvetch and adjacent creosote bush sites (table 2), these differences are typically small and fit

easily within the range of Mojave Desert soils that support creosote bush scrub communities (Graham and O'Geen 2010; Cox and others 1984; Romney and others 1973; Schlesinger and others 1996; Rundel and Gibson 1996). While the soil of milkvetch barrens tends to be marginally less fertile than adjacent creosote bush scrub (in other words, higher N and P, table 2), these differences are unlikely to be the source of vegetation differences because other Mojave Deserts soils are less fertile than milkvetch granite barrens but support creosote bush scrub communities (Schlesinger and others 1996). A more likely edaphic agent for the stunting of the vegetation of milkvetch barrens is soil moisture. Milkvetch barrens and adjacent creosote bush-dominated sites share the same abiotic conditions of precipitation and temperature, but differ appreciably in soil depth; 0 to 40 cm in milkvetch barrens versus greater than 100 cm in adjacent, creosote bush-dominated sites. Since the texture of soils in milkvetch and creosote bush sites are nearly identical (table 2), the shallow soils of milkvetch barrens are likely to have less total water holding capacity relative to adjacent deep soil creosote bush sites, resulting in a reduction in shrub cover and other plant metrics (figure 3). Previous studies of edaphic communities have reported decreases in soil moisture as soils become shallower, with a resulting decrease in plant cover (Baskin and others 1972; Sharitz and McCormick 1973; Meyer 1986).

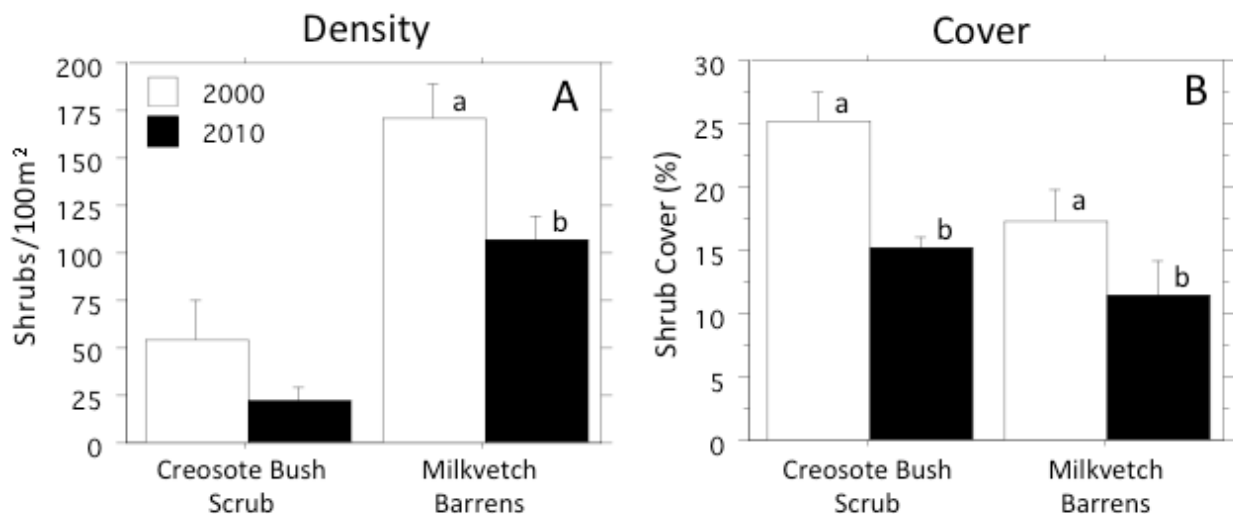


Figure 7. The effect of drought (1999-2010) on shrub density (A) and shrub cover (B) between milkvetch barrens and creosote bush scrub communities. Between 1999 and 2010, each community experiences declines in shrub density and cover, some of which were significant (*): milkvetch barrens density, $P = 0.0216$; milkvetch barrens cover, $P = 0.0029$ creosote bush scrub cover, $P = 0.0264$. Bars are means (+ SE).

Reductions in shrub cover on milkvetch barrens could occur in a number of ways (figure 8): through decreases in shrub size (figure 8B), through decreases in shrub density (figure 8C), or through some combination of change in both size and density of shrubs (figure 8D). In the case of milkvetch barrens, this reduction in cover has occurred through a proportional reduction in shrub size and inter-shrub distance (figure 8D). Consequently, on milkvetch barrens, shrub density increases and inter-shrub distance decreases relative to adjacent, creosote-dominated communities on deep alluvial soils.

Our previous seed bank studies have established that *A. jaegerianus* is a poor disperser, such that the dispersal of seed beyond host shrubs with seed-producing *A. jaegerianus* is extremely rare, and limited to near-by shrubs (Rundel and others 2009). High host shrub densities on milkvetch barrens (and consequent decreases in inter-shrub distance) could increase the likelihood of *A. jaegerianus* seed dispersal to other host shrubs, and as a result, restrict it to milkvetch barrens, where the probability of colonizing new shrubs is higher than in surrounding creosote bush-dominated communities. Hypothetically, low host shrub densities in creosote bush-dominated communities could create inter-shrub distances too great to support *A. jaegerianus* dispersal, effectively blocking expansion of *A. jaegerianus* into these areas. If *A. jaegerianus* population growth is limited by dispersal, and dispersal increases with increased shrub density, the drought-induced decreases in host shrub density observed since 1999 (figure 7A) may be a contributing factor in the failure of *A. jaegerianus* to recruit new plants in 11 years of observation.

Astragalus jaegerianus is a novel example of a second-order edaphic endemic whose distribution is indirectly controlled by edaphics through the effect of edaphics on its community of host shrubs. This indirect effect of edaphics is analogous to that of the cedar glade endemic *A. tennesseensis* A. Gray (Baskin and others 1972), in which shallow, rocky soils modify and reduce the dominant vegetation type into suitable habitat for *A. tennesseensis*. The degree to which indirect effects of edaphics on *A. jaegerianus* conform to models of edaphic endemism is unclear. On one level, *Astragalus jaegerianus* appears to conform to Gankin and Majors' (1964) "refuge model", in that *A. jaegerianus* is restricted to the shallow soils of milkvetch barrens that exclude the dominant creosote bush community because of a disadvantage:

insufficient soil moisture. Nevertheless, the shallow soils of milkvetch barrens are not an unambiguous "disadvantage" to *A. jaegerianus*, and so *A. jaegerianus* also appears to conform Meyer's (1986) "specialist" model, in that *A. jaegerianus* "is excluded from adjacent soils because its adaptation to its own soil has rendered it less able to survive on other types of soil." However, in the case *A. jaegerianus*, specialization does not occur in relation to the edaphics of granite barrens, but rather, to the shrub community that the edaphics of granite barrens produce. Ultimately, *A. jaegerianus* may not fit either the refuge or specialist model, and may require a new "indirect model" of edaphic endemism to explain its presence on granite barrens in central Mojave Desert.

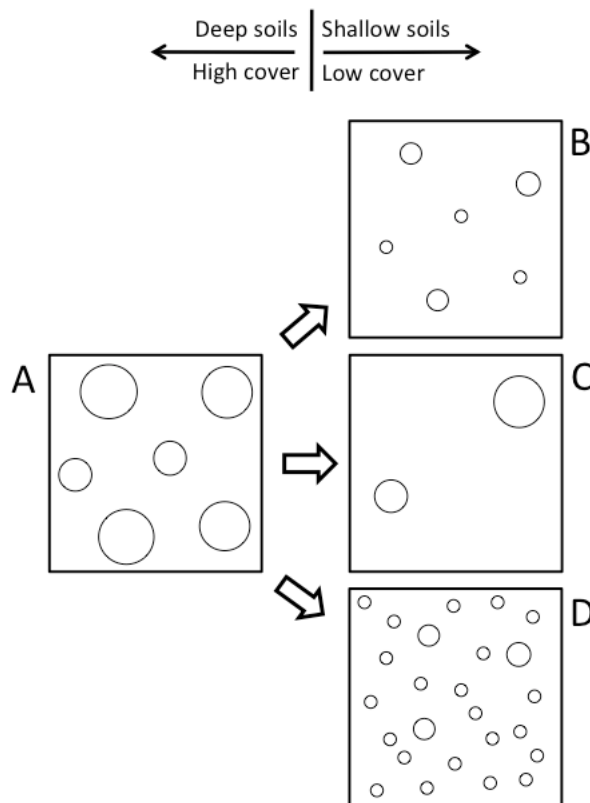


Figure 8. Diagram showing alternative edaphic-controlled transitions from a high-cover shrub community like creosote bush scrub, to low cover shrub community like that of milkvetch barrens in which shrub size has decreased (B), shrub density has decreased (C), or both shrub size and inter-shrub distance have decreased but the size and distance relationships between shrubs are maintained (D). Both community B and C are reasonable, *a priori* models of the effect of decreased soil moisture on community A, but community D more closely resembles the structure and organization of shrub communities on "milkvetch barrens".

CONCLUSIONS

1. The vegetation of “milkvetch barrens” in the central Mojave Desert (900 to 1200 m) is a desert rupicolous scrub that should be considered a distinct sub-community within Thorne’s “mixed desert scrub” because of its distinctive edaphically controlled vegetation structure, its limited distribution, and the presence of the edaphic endemic *A. jaegerianus*.
2. Results suggest that *A. jaegerianus* does not show a preference for host shrub, except that *Larrea tridentata* is significantly under-represented as a host shrub and so appears to be an unsuitable host shrub for *A. jaegerianus*. This unsuitability may be due to *Larrea*’s architecture, which is significantly taller than suitable host shrubs, and too tall and open to allow *A. jaegerianus* to climb through and reach its canopy.
3. Drought condition since 1999 have led to decreases in density and cover in both milkvetch barrens and adjacent creosote bush-dominated communities, but the density of host shrubs in milkvetch barrens in 2010 remain twice that of pre-drought creosote bush-dominated communities. Drought-induced decreases in host shrub density may be a contributing factor in the failure of *A. jaegerianus* to recruit new plants since 1999.
4. The shrub community on milkvetch barrens is composed of smaller shrubs at a significantly higher density than in the surrounding creosote bush dominant community. Soil depth is likely to be the edaphic factor responsible for the stunted vegetation of milkvetch barrens, because their shallow soils have less total water holding capacity relative to adjacent deep-soil creosote bush sites, resulting in a reduction in shrub cover and other plant metrics.
5. The higher shrub density of milkvetch barrens reduces inter-shrub distance, which is hypothesized to increase *A. jaegerianus* dispersal and population growth. Reciprocally, low host shrub densities in adjacent creosote bush-dominated communities could create inter-shrub distances too great to support *A. jaegerianus* dispersal, effectively blocking expansion of *A. jaegerianus* into these areas.

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