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Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size

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Abstract Positive interactions often play an important role in structuring plant communities and increasing biological diversity. Using three scales of resolution, we examine the importance of a long-lived desert tree, ironwood (*Olneya tesota*), in structuring plant communities and promoting biological diversity in the Sonoran Desert. We examined the positive effects of *Olneya* canopies of different sizes on plant communities in mesic and xeric habitats throughout the central Gulf Coast subregion of Sonora, Mexico. In xeric sites, *Olneya* canopies had strong positive effects on plant richness and abundance, and small positive effects on the size of plants, underscoring the role of facilitation in extreme environments. In mesic sites, *Olneya* canopies had very little effect on perennials and a negative effect on ephemeral richness, suggesting predominantly competitive effects in this less stressful environment. Overall, *Olneya* canopies increased biological diversity where abiotic stress was high, but did not increase diversity in more mesic areas. Thus *Olneya* canopies caused consistent shifts in plant-community structure among xeric and mesic sites, but not when these landscapes were combined. Benefactor size also mediated positive interactions, with larger *Olneya* canopies supporting larger perennials in both xeric and mesic sites. Thus stress gradients and benefactor size both influenced the balance of facilitative and competitive effects under nurse-plant canopies, and the spatial scale at which facilitative effects shape community structure.

Keywords Benefactor size · Ecological scaling · Facilitation · *Olneya* · Stress gradients

Introduction

The relative importance of processes that structure plant communities and maintain biological diversity has been a primary focus in community ecology (Abrams 1995; Connell 1978; Hacker and Gaines 1997; Huston 1979, 1994; Janzen 1970; Lubchenco 1978; MacArthur and Levins 1964, 1967; Menge and Sutherland 1976, 1987; Paine 1966; Pianka 1974; Tilman 1982; Tilman et al. 1996). Early work focused on competition (reviewed by Connell 1983; Connell and Slatyer 1977; Goldberg and Barton 1992; Keddy 1989; Schoener 1983), but recent research has examined the importance of positive interactions in structuring communities and promoting biological diversity (Bertness and Callaway 1994; Callaway 1995, 1997, 1998; Callaway and Walker 1997; Hacker and Bertness 1999; Hacker and Gaines 1997; Hector et al. 1999). The local effects of facilitation have been well-documented: Benefactor species can influence recruitment, growth, and spatial associations of beneficiary species through a variety of pathways, both direct (Bruno and Kennedy 2000; Dawson 1993; Shreve 1931; Shumway 2000; Went 1942) and indirect (Callaway 1992a; Hacker and Bertness 1995; Levine 1999). However, few authors have examined the consistency of these local effects or the ability of benefactors to provide stable microclimates at larger spatial scales. If benefactors have consistent effects on plant community structure, many beneficiaries may depend on these positive effects throughout large portions of their range.

Desert plant communities are excellent systems with which to examine large-scale effects of positive interactions. Physical stress is severe, and stress gradients arise with variation in water availability, with high abiotic stress occurring on dry uplands away from ephemeral watercourses. Suzan (1994) found that growth rates of Sonoran Desert trees were significantly lower in upland

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sites when compared to more mesic sites along ephemeral watercourses, clearly indicating the presence of a gradient in abiotic stress (Grime 1979). In the Sonoran Desert, larger plants often have strong facilitative effects on other species (McAuliffe 1984; Parker 1988; Turner et al. 1966; Valiente-Banuet et al. 1991). Indeed, one of the first clear examples of the role of positive interactions among plants was the “nurse plant” effect (Shreve 1931, 1951) in which larger desert trees such as palo verde (*Cercidium* spp.), mesquite (*Prosopis* spp.) and ironwood (*Olneya tesota*) facilitate the germination and seedling survival of other species (Burquez and Quintana 1994; Hutto et al. 1986; McAuliffe 1984, 1988; Shreve 1951; Suzan et al. 1996; Tewksbury and Petrovich 1994). *Olneya*, a monospecific genus, is the longest-living tree in the Sonoran Desert, often living over 800 years (Suzan 1994). The tree attains a canopy size >12 m in diameter (Suzan et al. 1996) and retains its leaves throughout the year, providing a large area under its canopy that is consistently buffered from temperature extremes over many generations of understory plants. Indeed, previous work has found that plant species richness and abundance beneath *Olneya* canopies are significantly greater than in surrounding areas (Burquez and Quintana 1994; Suzan et al. 1996; Tewksbury and Petrovich 1994). *Olneya* also grows in a wide variety of habitats within the Sonoran Desert, occurring with mesquite and palo verde along relatively mesic ephemeral watercourses, and also growing on highly xeric plains where other trees are absent. This broad gradient of water stress allows us to examine the conditions under which *Olneya* canopies affect plant community structure across large spatial scales. In addition, *Olneya* canopy sizes vary substantially within a given area, allowing examination of the effect of canopy size on understory plant communities.

Materials and methods

Sampling

We established 10 1-ha study sites in the Central Gulf Coast subregion (Shreve 1951; Turner and Brown 1982) of Sonora, Mexico (Fig. 1). For a detailed description of each study site, see Tewksbury and Petrovich (1994). Five of these sites were located along drainage channels of ephemeral watercourses (mesic sites – low water stress), and five were located on dry upland bajadas (xeric sites – high water stress). At each site, we measured the canopy area of each *Olneya* greater than 1.5 m tall. We considered the area underneath each *Olneya* canopy that we measured to be a plot, and we established an equal number of control plots at each site. Control plots were randomly placed within the site and were equal in size to the mean plot size for *Olneya* trees surveyed on the site (Tewksbury and Petrovich 1994). Within each plot (both *Olneya* and control), we counted all ephemeral and perennial plants by species and measured their canopy sizes. Where over 100 individuals of a single species were encountered in the same plot, we measured the canopy size of a random subset of 20 individuals.

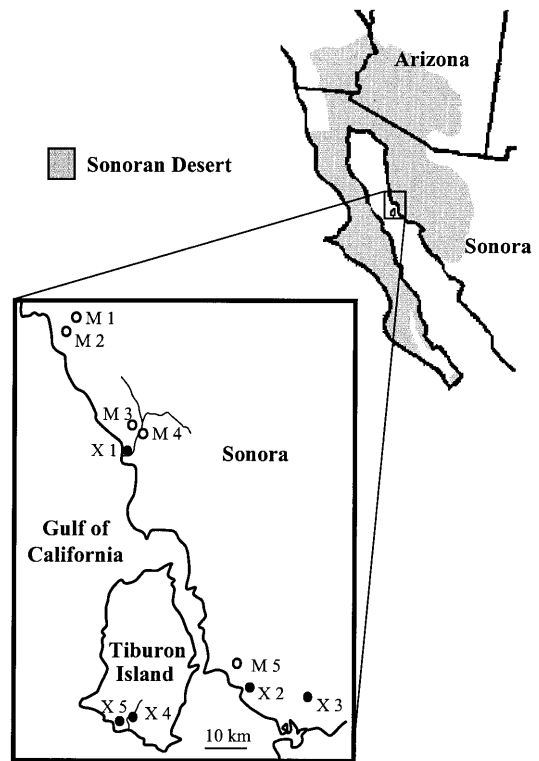


Fig. 1 Map of the study area, spanning 645 km² along the coast of the Gulf of California in Sonora, Mexico. Xeric sites are closed circles (X1–X5), mesic sites are open circles (M1–M5)

Data analysis

Effect of spatial scale

To examine the effects of *Olneya* on understory species, we used Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) to ordinate *Olneya* plots and control plots based on species composition and density within each plot. DCA separates sources of variation into different axes, allowing the examination of different factors on overall community structure. The factors explaining the greatest amount of variation in the data separate plots along the primary DCA axis, while factors explaining a lesser amount of variation separate plots along the secondary axis of variation. We measured the effect of *Olneya* at three scales: landscape, site condition (mesic versus xeric habitats), and the individual site. At the landscape scale, we grouped all plots from all sites into a single DCA to determine if *Olneya* plots were consistently different from control plots across all xeric and mesic sites spanning over 100 km of coastal Sonora. At the site condition scale, we separated low-water-stress (mesic) sites from high-water-stress (xeric) sites and ordinated each in separate DCAs to determine if *Olneya* consistently structured plant communities across large spatial scales once the effect of water stress was removed. Finally, at the smallest scale (the site scale), we conducted separate DCAs for each of the ten sites to determine the effect *Olneya* canopies using only the species pool present within each site.

Using the results of these ordinations, we examined sources of variation in plant community structure at each scale using ANOVA models. At the largest scale, our ANOVA model included water stress (xeric or mesic), the presence of *Olneya*, and the interaction. We included water stress as a factor because we predicted that water availability would be an important source of variation in plant community structure at this level. At the next smallest scale where we ordinated xeric and mesic sites separately, we included site and the presence of *Olneya* as factors, as well as the in-

teraction term. Including site as a variable allowed us to isolate the effect of inherent variation among sites within mesic and xeric areas. At the site scale, we compared plant community structure between *Olneya* and control plots within each site using one-way ANOVA models. Conducting a hierarchical analysis in this fashion allowed us to determine the extent to which *Olneya* canopies cause consistent and predictable changes in plant-community structure under their canopies.

All ordinations were conducted using PC-ORD (McCune and Mefford 1995). With the exception that we downweighted rare species, the default settings were used for each DCA: axes were rescaled with a threshold of zero and the number of segments considered was 26. All other analyses were conducted using SPSS version 10.05 (SPSS 1999).

Effect of water stress and canopy size

We used General Linear Models to examine the facilitative effects of *Olneya* canopies as a function of water stress (xeric versus mesic sites) and beneficiary type (perennial versus ephemeral vegetation). We included beneficiary type in our models because the stable shade provided by *Olneya* canopies may have different effects on long-lived perennials and on ephemeral plants, and because the exceptionally high densities of ephemeral plants would have obscured changes in perennials. We compared the richness and abundance of perennial and ephemeral plants in control and *Olneya* plots, and examined the interaction between plot type (control or *Olneya*) and water stress (mesic or xeric sites) to determine how water stress influenced the balance between facilitation and competition under *Olneya* canopies. To examine individual differences among *Olneya* and control plots in both xeric and mesic sites, we used the Hochberg GT2-method (Hochberg 1974). This post-hoc testing method provides a conservative estimate of individual differences, correcting for the inflated significance associated with multiple comparisons, and is appropriate where sample sizes are unequal (Sokal and Rohlf 1995). To examine the effects of *Olneya* canopies on the size of ephemeral and perennial species, we calculated the percentage difference in the average size of plant species occurring under canopies from their average size in open (control) plots in the same site. We used one-sample *t*-tests to test for significant deviations from zero difference. To determine if absolute size differences between plants growing in the open and plants growing under *Olneya* were different between xeric and mesic sites, we used *t*-tests. In both tests, we used only species that occurred in both *Olneya* and control plots. Lastly, we examined the extent to which *Olneya* canopies provided habitat

for species not found in control plots on the same site – the influence of *Olneya* canopies on site level richness. For this analysis, we determined the proportion of species detected on the site that were found only under *Olneya* canopies, and the proportion found only outside these canopies (in control plots). To determine the effect of *Olneya* canopy size on facilitative strength, we regressed richness, abundance, and change in size of both perennials and ephemerals against *Olneya* canopy size (m²) in both xeric and mesic sites. We tested for differences in the effect of canopy size between xeric and mesic sites using parallelism tests (canopy size by water stress interaction). Variables were log- or arcsine-square-root transformed to meet assumptions of parametric tests when necessary.

Results

Effect of spatial scale

At the landscape scale, the presence of *Olneya* did not explain a significant amount of variation in plant community structure along either the primary ($P=0.923$) or secondary DCA axes ($P=0.633$) (Fig. 2, Table 1). Instead, water stress was highly significant along the primary axis (Table 1; $P<0.0001$), suggesting that much of the variation in plant communities at this scale is due to differences in water availability among sites, rather than the presence of *Olneya*. The interaction between water stress and *Olneya* was also insignificant (axis 1, $P=0.162$; axis 2, $P=0.334$).

When we ordinated xeric and mesic plots separately (site condition scale) the presence of *Olneya* had a large effect on plant community structure despite significant variation along both axes attributable to differences between sites within site conditions (all $P<0.0001$). In xeric sites, the effect of *Olneya* canopies was large along both axes (Table 1, Fig. 3A; P 's <0.004); in mesic sites the effect was large along the primary axis (Fig. 3B; $P=0.003$) but not the secondary axis (Fig. 3B; $P=0.058$).

The differences between plant communities under *Olneya* canopies and plant communities in control plots

Table 1 ANOVA summary table showing variance ratios, significance ($*P<0.05$, $**P<0.01$, $***P<0.001$) and error mean square for the effects of water stress, site and *Olneya* canopies on the primary and secondary DCA axis scores at both the landscape scale (all

plots together) and site condition scales (plots in xeric and mesic sites run separately). At the landscape scale, water stress is included as a fixed effect; at the site condition scale, site is included as a fixed effect

	Landscape scale variance ratios			Site condition scale variance ratios					
	df	Primary axis	Secondary axis	Xeric			Mesic		
				df	Primary axis	Secondary axis	df	Primary axis	Secondary axis
Water stress	1	104.54***	0.499	–	–	–	–	–	–
Site	–	–	–	4	68.27***	39.07***	4	27.66***	30.12***
<i>Olneya</i>	1	.01	0.229	1	10.34**	9.01**	1	9.44**	3.74
Water stress-by- <i>Olneya</i>	1	1.97	0.936	–	–	–	–	–	–
Site-by- <i>Olneya</i>	–	–	–	4	2.06	1.41	4	1.37	4.86***
Error mean square	283	3926.30	4025.21	112	2282.26	2803.76	155	2890.98	1647.56

Table 2 ANOVA summary table showing variance ratios, significance ($*P<0.05$, $**P<0.01$, $***P<0.001$) and error mean square for the effects of water stress (xeric versus mesic sites) and the presence of an *Olneya* canopy on the richness and abundance of perennials and ephemerals (Fig. 5A–D)

	df	Richness variance ratios		Abundance variance ratios	
		Perennial	Ephemeral	Perennial	Ephemeral
Water stress	1	31.56***	14.61***	5.70*	3.30
<i>Olneya</i>	1	34.21***	7.64**	10.37**	1.48
Water stress-by- <i>Olneya</i>	1	9.50**	3.19	3.20	2.18
Error mean square	283	6.77	3.86	286.90	79,011.42

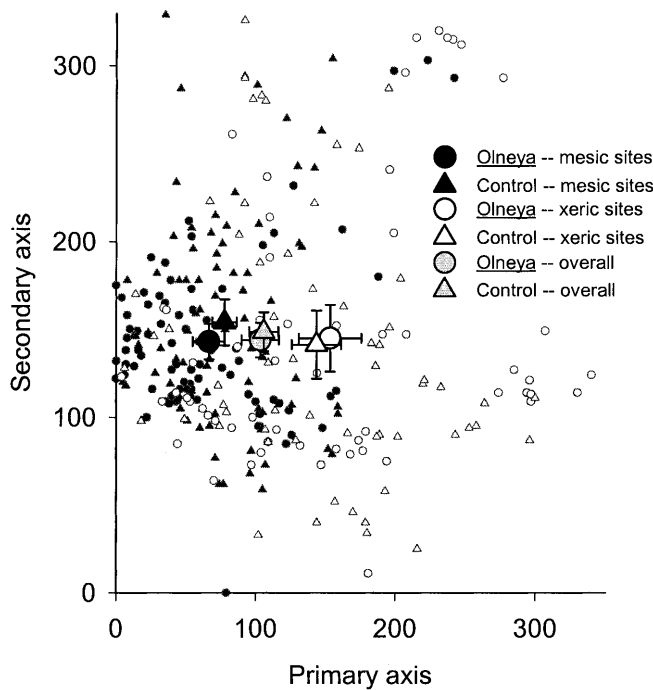


Fig. 2 Results of the Detrended Correspondence Analysis (DCA) ordination conducted across all plots (landscape-level ordination). Raw scores along axes 1 and 2 are shown for all plots (small symbols), and overall mean scores and 95% confidence intervals are shown for *Olneya* and control plots in mesic sites, xeric sites, and all sites combined (large symbols)

was also apparent at six of the ten individual sites when we controlled for variation due to differences in water stress and site factors by conducting separate ordinations at each site (Fig. 4). *Olneya* plots were more often different than control plots in xeric sites (4/5) than in mesic sites (2/5), paralleling the trend seen when plots were ordinated at the larger scale of site condition.

Effect of water stress

Perennial and ephemeral plants were generally more diverse and abundant in mesic sites (Table 2, perennial and ephemeral richness $P<0.001$, perennial abundance $P=0.018$, ephemeral abundance $P=0.07$). This pattern was almost entirely due to differences in control plots, where richness and abundance were generally greater in mesic areas (Fig. 5A–D white bars; perennial richness, $P<0.006$; perennial abundance, $P<0.021$, ephem-

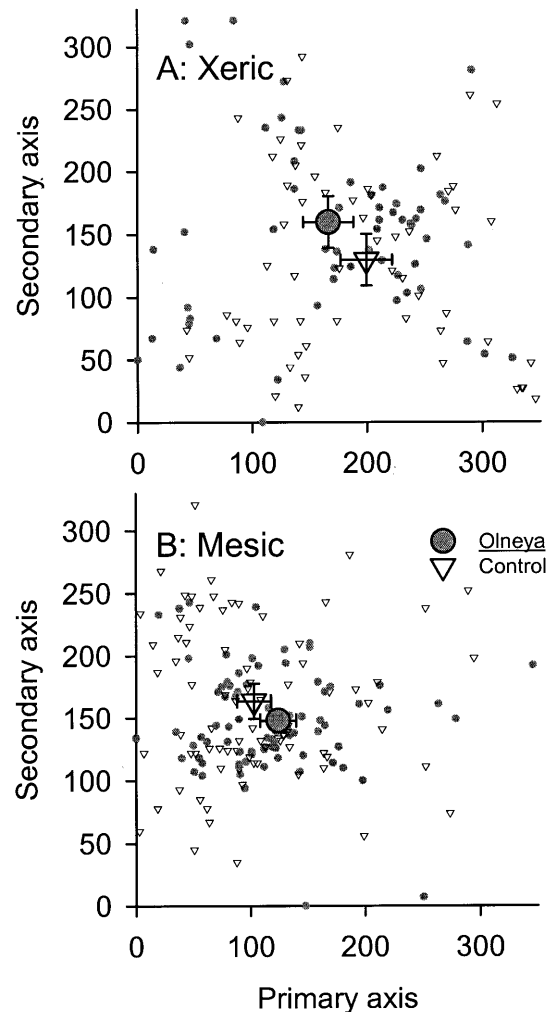


Fig. 3 Results of the DCA ordination conducted across all xeric plots (A) and all mesic plots (B). Raw scores along axes 1 and 2 are shown for all *Olneya* plots (small dark-gray circles) and all control plots (small gray triangles). Overall mean score and 95% confidence intervals are shown for *Olneya* plots and control plots (large symbols)

eral abundance $P=0.118$). In contrast, under *Olneya* canopies, richness and abundance were not significantly different between mesic and xeric plots (Fig. 5A–D gray bars; all $P>0.36$). However, DCA of plant community composition under *Olneya* canopies showed significant differences between xeric and mesic environments (ANOVA $F=54$, $P<0.001$). Thus, while the number of species and individuals under *Olneya* canopies may remain fairly uniform,

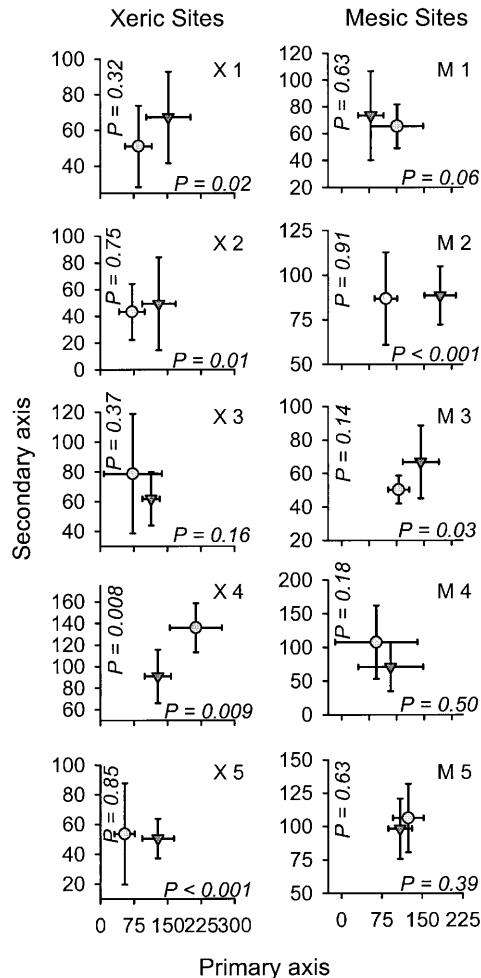


Fig. 4 Mean DCA axis 1 and 2 scores for *Olneya* (dark gray triangles) and control (light gray circles) plots from ordinations conducted at each site. Error bars are 95% confidence intervals. *P* values are for difference between *Olneya* and control plots

there are significant differences in the community composition between xeric and mesic sites.

The relatively constant values for richness and abundance under *Olneya* canopies and the large variation in these values in control plots resulted in differences in the facilitative effects of *Olneya* canopies between high and low water stress sites (Table 2; interaction terms: perennial richness $P=0.002$, perennial abundance $P=0.075$, ephemeral richness $P=0.075$, ephemeral abundance $P=0.141$). In xeric sites, facilitation of perennials was strong; richness and abundance were higher under *Olneya* canopies (Fig. 5A, C, $P<0.007$) while ephemerals were unaffected (Fig. 5B, D, $P>0.35$). In contrast, in mesic sites there was no difference between *Olneya* and control plots in perennial richness ($P=0.19$), perennial abundance ($P=0.85$) or ephemeral abundance ($P=1$). Further, ephemeral richness was significantly lower under *Olneya* canopies in mesic plots (Fig. 5B, $P=0.003$).

The effect of *Olneya* canopies on site-level diversity differed strongly as a function of both water stress and beneficiary type, having stronger effects in xeric areas

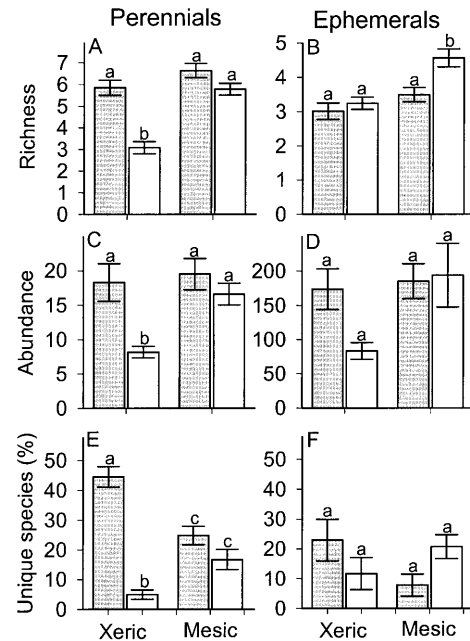


Fig. 5 Richness (A, B), abundance (C, D) and the proportion of species in a site found exclusively under *Olneya* canopies or in control plots (E, F) for perennials (left) and ephemerals (right) for xeric and mesic sites. Gray bars are *Olneya* plots; white bars are control plots. Mean \pm one standard error from estimated marginal means are shown. Letters above bars indicate differences significant at the $P=0.05$ level from GT2-method post-hoc tests. Actual significance levels are reported in the text

Table 3 ANOVA summary table showing variance ratios, significance ($*P<0.05$, $**P<0.01$, $***P<0.001$) and error mean square for the effects of water stress (xeric versus mesic sites) and beneficiary type (perennial versus ephemeral) on the number of species found exclusively under *Olneya* canopies or exclusively in control plots (Fig. 5E, F)

	<i>df</i>	<i>Olneya</i>	Control
Water stress	1	13.84**	8.51*
Beneficiary type	1	18.41**	0.91
Water stress-by-beneficiary type	1	0.12	0.32
Error mean square	16	104.67	82.61

than mesic areas (Table 3; $P=0.002$) and stronger effects on perennials than ephemerals (Table 3; $P=0.001$). At xeric sites an average of 45% of perennial species were found only under *Olneya* canopies, whereas fewer than 5% of perennial species were found only in control plots (Fig. 5E, $P<0.0005$). In contrast, there was no difference in the proportion of ephemeral species found exclusively under *Olneya* canopies or exclusively in control plots in these same xeric sites (Fig. 5F, $P=0.44$). In mesic sites, there was no significant difference in the proportion of perennial or ephemeral species found exclusively under *Olneya* canopies or exclusively in control plots (Fig. 5E, F, $P>0.29$).

When all plots are considered together, perennial and ephemeral plant species found under *Olneya* canopies

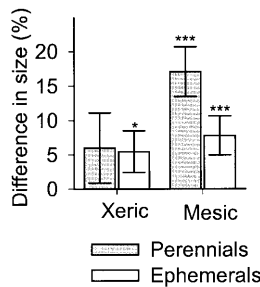


Fig. 6 Difference in the size of perennial and ephemeral beneficiaries growing under *Olneya* canopies (percentage larger than average size of the same species growing in control plots). Asterisks indicate significant difference in size of vegetation under canopies when compared to control plots (* $P < 0.05$, *** $P < 0.0001$)

were larger than their counterparts in open plots (perennials one-sample $t = 3.3$, $P = 0.001$, ephemerals one-sample $t = 4.1$, $P < 0.001$). However, this overall effect was driven primarily by large differences in vegetation size in mesic sites, where perennials were 15% larger under *Olneya* (Fig. 6, one-sample $t = 4.7$, $P < 0.001$) and ephemerals were 7% larger (one-sample $t = 2.7$, $P = 0.004$). In xeric sites, there was no significant effect for perennials (Fig. 6; one-sample $t = 1.2$, $P = 0.124$) and only a marginally significant effect for ephemerals (one-sample $t = 1.8$, $P = 0.04$).

Effect of *Olneya* canopy size

Olneya canopies ranged in size from 1.54 m² to 162 m², covering a mean area of 28.3 m² (SEM=2.2). However, the majority of the canopies were smaller than the mean (median=18 m²). The size of *Olneya* canopies did not differ between xeric and mesic sites ($t = 1.07$, $P = 0.29$).

Perennial plants were more strongly affected by differences in *Olneya* canopy size than ephemeral plants. *Olneya* canopy area had a significant positive effect on beneficiary richness (Fig. 7A; xeric $R^2 = 0.17$, $B = 0.25$, $P = 0.001$; mesic $R^2 = 0.15$, $B = 0.22$, $P < 0.001$), abundance (Fig. 7C; xeric $R^2 = 0.29$, $B = 0.51$, $P < 0.001$; mesic $R^2 = 0.20$, $B = 0.39$, $P < 0.001$), and size of perennials (Fig. 6E; xeric $R^2 = 0.181$, $B = 0.22$, $P = 0.001$; mesic $R^2 = 0.092$, $B = 0.10$, $P = 0.006$; slope test $F = 4.4$, $P = 0.04$). In contrast, ephemeral richness was unaffected by *Olneya* canopy size (Fig. 7B; $R^2 < 0.001$, $B < 0.02$, $P > 0.7$); and ephemeral abundance increased only in xeric sites (Fig. 7C; xeric $R^2 = 0.09$, $B = 0.52$, $P = 0.012$; mesic $r^2 = 0.007$, $B = 0.18$, $P = 0.217$). While abundance was positively related to canopy area, the slopes of all these relationships in both xeric and mesic sites were far less than one ($t > 5$, $P < 0.001$), indicating that increases in abundance under larger trees did not keep pace with increases in area under the canopy. Thus, plant density actually decreased under larger canopies. The slopes of the relationships between canopy size and richness and abundance (Fig. 7A–D) did not differ significantly between xeric and mesic sites (parallelism tests; perennials $P > 0.37$, ephemerals $P > 0.17$).

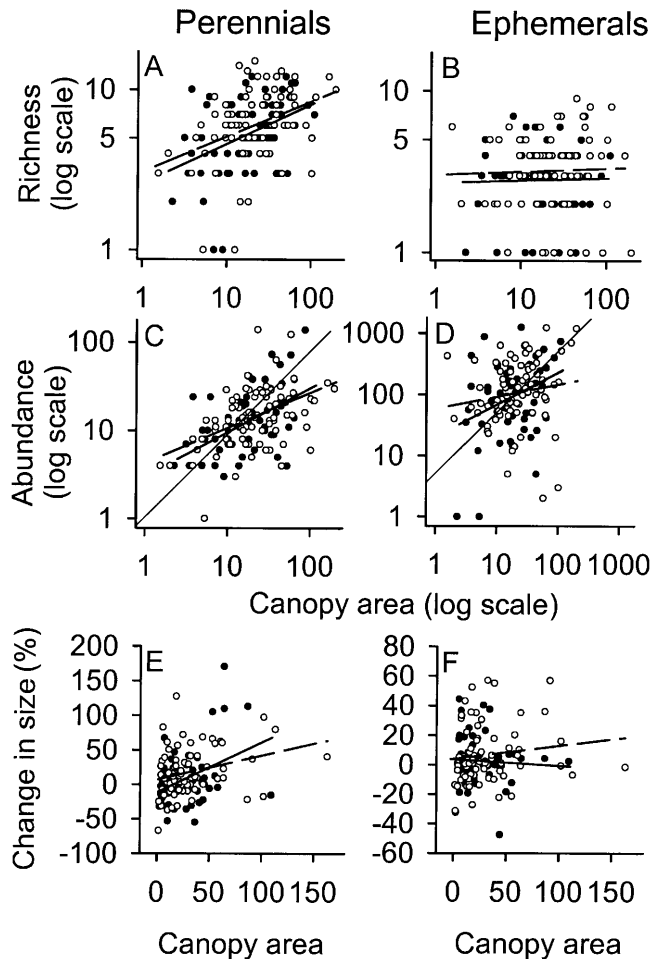


Fig. 7 Richness (A, B), abundance (C, D) and percent difference in size (E, F) of perennials (left) and ephemerals (right) under *Olneya* canopies in xeric (closed circles) and mesic (open circles) sites as a function of the size of each *Olneya* canopy (m²). Lines are regression lines for xeric (solid line) and mesic (dashed line) values. Richness and abundance figures (A–D) are plotted on a log–log scale. For abundance (C, D), a 1-to-1 line is included to show the slope of the relationship if vegetation density remained constant with increasing *Olneya* canopy size

The size of perennial plants showed a significant positive relationship with increases in canopy area in both xeric and mesic sites, while ephemeral size showed no relationship with canopy area in either xeric or mesic sites (Fig. 7F; xeric $R^2 = 0.04$, $B = -0.04$, $P = 0.64$; mesic $R^2 = 0.02$, $B = 0.09$, $P = 0.20$).

Discussion

The shaded canopies of long-lived *Olneya* trees can have a strong effect on the structure of Sonoran Desert plant communities, causing large increases in plant species richness and abundance in the most xeric habitats of the Sonoran Desert. Such effects of tree canopies in desert regions have served as a classic example of facilitation (Shreve 1951), and a number of studies have documented the local effect of *Olneya* canopies on desert plants

(Burquez and Quintana 1994; Suzan 1994; Suzan et al. 1996; Tewksbury and Petrovich 1994). Our results suggest that these local facilitative effects of *Olneya* canopies are largely confined to the more xeric habitats within the Sonoran Desert, away from ephemeral streams. However, within both mesic and xeric habitats, the effects of *Olneya* canopies are consistent across study sites separated by as much as 100 km. Within these habitat types, the effects of *Olneya* canopies on beneficiaries appears to be modified by *Olneya* canopy size, and whether the beneficiary plants are perennial or ephemeral.

Water stress and benefactor size had independent effects on facilitation. These effects have been documented in a number of xeric environments (Belsky 1994; Fuentes et al. 1984; Greenlee and Callaway 1996; Hillier 1990; Kellman and Kading 1992). However, these two factors acted very differently on perennial plants than on ephemeral plants in our study, leading to different effects on richness, abundance and plant size under different conditions. The conditional nature of facilitative effects under this long-lived tree thus supports the importance of considering multiple factors when examining the overall importance of nurse-plant canopies in structuring plant communities (Bertness et al. 1999; Callaway and Walker 1997).

Water stress has been repeatedly identified as one of the strongest abiotic gradients in the Sonoran Desert (De Jong and Klinkhamer 1988; Franco and Nobel 1989; Suzan 1994; Turner et al. 1966; Valiente-Banuet and Ezcurra 1991), and our data support this finding, as differences in water stress completely masked the facilitative effect of *Olneya* canopies at the largest (landscape) scale of analysis (Fig. 2). However, when large-scale differences in moisture were controlled, plant communities under *Olneya* canopies were consistently different from those in control plots (Fig. 3), despite large differences in community composition between sites. This effect was greater in xeric sites, where water stress in the open was more extreme (Figs. 3, 4). In these areas, the richness and abundance of both perennials and ephemerals in the open were consistently lower than in mesic sites. However, richness and abundance were similar under *Olneya* canopies across this water stress gradient (Fig. 5), suggesting that the environment under *Olneya* canopies may act as an environmental buffer (Suzan et al. 1996), providing a relatively homogeneous environment to beneficiaries. This buffering appears to lead to differences in the importance of facilitation as a function of ambient levels of water stress; in areas of higher abiotic stress, the vegetation under *Olneya* canopies contributes more to site-level diversity (Fig. 6E, F) than in areas with low abiotic stress. Thus, as predicted by Bertness and Callaway (1994) and more recently by Hacker and Gaines (1997) the positive influence of *Olneya* canopies play a larger role in maintaining plant species richness and abundance as abiotic stress increases.

The shaded microenvironment created by *Olneya* canopies reduces air and soil temperature in summer and in-

creases air and soil temperature in winter (Suzan et al. 1996). This stabilization of soil surface temperatures is critical for seedling establishment and growth, as mortality due to desiccation and heat stress are often highest early in the life stage of desert plants (Franco and Nobel 1989; Nobel 1980; Valiente-Banuet and Ezcurra 1991). The shade provided by *Olneya* canopies also affects adult plants by increasing available soil moisture and decreasing available light. The effect of these changes on the plant community depends on the extent to which light and/or water are limiting the establishment and growth of plants (Holmgren et al. 1997). This in turn varies depending on the life history of the plants involved, including their patterns of allocation, photosynthetic pathway, timing of water use, and competitive environment (Callaway 1992a, 1992b, 1995; Shumway 2000). Indeed, *Olneya* canopies had strong facilitative effects on perennials in xeric and mesic areas (Fig. 5A), while facilitative effects on ephemerals were limited to xeric areas and were never as strong as the effects on perennials (Fig. 5B, D). These differences may be predicted based on the life history differences between these groups. Ephemerals often avoid drought-stress by investing heavily in rapid development and early flowering, so that they are only growing when water is available. In contrast, perennials may be more sensitive to differences in water availability, particularly during early development (Valiente-Banuet and Ezcurra 1991), as they cannot avoid the driest periods, thus we might expect the increased water availability under *Olneya* canopies to have larger effects on perennials. In addition, water and light limitation may change competitive environments under *Olneya* canopies in different ways. In more mesic areas, individual plants were significantly larger under *Olneya* canopies than in control plots, suggesting that the shaded microenvironment benefits established plants more in areas where water stress is less limiting. This facilitation of plant growth may limit the entry of additional individuals and species under the canopies of *Olneya* in mesic sites, reducing the facilitative effects on plant richness and abundance. In contrast, plant size was only marginally greater under *Olneya* canopies than in control plots in xeric areas (Fig. 6), but the facilitative effects of *Olneya* canopies on plant richness and abundance were strong (Fig. 5).

The facilitative effects of long-lived nurse plants such as *Olneya* also change as the trees grow and age, and competitive effects between understory plants may begin to exclude entry by new individuals. Our finding that larger canopies had a higher richness of perennials than smaller trees may reflect a typical species-area curve, but it is also probably a function of increasing age of the nurse-plant. Larger trees have more time to accumulate nutrients and a larger seed bank, by both collecting leaves, soil, and wind-dispersed seeds (Callaway et al. 1991; Carrillo et al. 2000), and accumulating seeds through the foraging behavior of birds, which use trees as roosts and nesting substrate and disperse seeds beneath the canopy (Archer et al. 1988; Dean et al. 1990;

Kellman and Kading 1992; McClanahan and Wolfe 1993; Milton et al. 1998; Tewksbury et al. 1999). The increase in the size of perennials under larger *Olneya* canopies potentially explains the finding that perennial abundance did not increase in proportion to the increased area available under larger canopies. Once established, growing perennials may limit the number of additional individuals that can become established under larger *Olneya* canopies (Suzan 1994). As ephemerals are by nature short-lived, the age of the *Olneya* and size of the canopy has no effect on their size (Fig. 7F), but increased perennial size may still limit the density of ephemerals under older, larger *Olneya* canopies (Fig. 7D).

Community importance

Olneya canopies had the largest effect on community structure and species richness where water stress was high. In these areas, *Olneya* is often the only large arborescent plant, and thus the shade under *Olneya* canopies is particularly important for other species. In these areas, a large proportion of the species present were found only under *Olneya* canopies, making it a clear example of a keystone habitat-modifier species (Mills et al. 1993; Power and Mills 1995). In more mesic areas, the effects of *Olneya* on community structure were less dramatic, and the canopy may have had both competitive and facilitative effects. Along these ephemeral streams, mesquite and palo verde are also abundant, providing shaded microclimates, and, for species simply requiring this shade, the species may be less important than its function (Lawton 1991, 1994; Walker 1992). However, Suzan (1994) found that where *Olneya* occurred with other trees, many shrubs and cacti were associated with *Olneya* canopies significantly more often than with the canopies of other shade-providing species. Thus even in more mesic areas, *Olneya* may be disproportionately important.

While many studies have documented the importance of stress gradients in determining the balance of facilitation and competition (Bertness and Hacker 1994; Bertness and Yeh 1994; Chapin et al. 1994; Greenlee and Callaway 1996; Hacker and Bertness 1999; Tielborger and Kadmon 2000) the majority of these studies have focused on species-specific interactions; there have been fewer attempts to explicitly examine the effect of nurse-plants in determining overall community structure and diversity, particularly over large geographic areas (but see Hacker and Bertness 1999; Hacker and Gaines 1997; Hay 1986). Our results corroborate earlier work suggesting that physical stress gradients are critical in determining the overall effect of nurse-plants (Bertness and Callaway 1994), and they also suggest that the community effect of nurse-plants is highly dependent on ambient stress levels, and the degree of amelioration provided by nurse-plant canopies (Holmgren et al. 1997). The importance of positive, facilitative interactions in structur-

ing plant communities may depend on the interactions between multiple stress gradients and the structure of dominant species providing relief from these stressors (Bertness et al. 1999; Bruno and Kennedy 2000). These factors may in turn influence the scale at which facilitative effects are apparent. The explicit consideration of nurse-plant size and stress gradients will aid in our understanding of positive interactions and the scale at which they occur, especially in arid regions where water and light stress may dominate community structure.

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