Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture

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Abstract

This study samples 247 saguaros (*Carnegiea gigantea*) and their nurses in 30 populations in the northern Sonoran Desert to determine whether saguaros are randomly distributed beneath their nurses' canopies. Saguaro–nurse association patterns are compared across three nurse groups distinguished by canopy architecture characteristics (leguminous trees, small dense *Ambrosia* spp. shrubs, and the larger, open-canopied shrub *Larrea tridentata*).

For all three nurse types, saguaros are significantly clustered near the center of their nurse's base. Clustering varies with nurse architecture, as saguaros are most tightly clumped under the most open-canopied species (*L. tridentata*), as more than 80% of saguaros were under the innermost 10% of *L. tridentata*'s subcanopy area. Saguaros showed the least basal clustering about tree nurses, though not significantly less than *Ambrosia* spp. nurses. More saguaros establish under *Ambrosia* relative to its cover in sampled populations, while saguaros were underrepresented under *L. tridentata*.

All analyses suggest that *L. tridentata* is an inferior nurse for saguaros. Different canopy architecture influences the extent of ground available to a nursed species to benefit from, for establishment and survival. While herbivory, rodents or other factors may play a role in these

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patterns, ultimately microclimate differences are the most likely factor shaping cacti–nurse associations in the harsh desert environment.

1. Introduction

Many plant species are associated with nurse plants (Valiente-Banuet and Ezcurra, 1991; Gass and Barnes, 1998; Jurena and Van Auken, 1998; Reay and Norton, 1999) or nurse rocks (e.g. Bowers and Pierson, 2001). The saguaro cactus (*Carnegiea gigantea* (Engelm.) Britt. and Rose) and other species found in harsh desert environments (McAuliffe, 1986; Nabhan and Suzan, 1994; Suzan et al., 1996) rely on these associations, particularly during the first years of life when survivorship is very low (Steenbergh and Lowe, 1977, 1983). Nurse plants are typically other perennial species that provide benefits to the 'nursed' individual through the modification of subcanopy microclimate, by providing shade (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991), reducing daytime and summer high temperatures (Franco and Nobel, 1989), reducing night-time and winter heat loss beneath their canopy (Nobel, 1980a; Drezner and Garrity, 2003), reducing soil surface temperatures (Franco and Nobel, 1988, 1989), reducing wind (Parker, 1989), by protecting seedlings from browsing animals (Niering et al., 1963; McAuliffe, 1984), and adding nutrients to the soil (Franco and Nobel, 1989; Franco-Pizana et al., 1996). All of these effects potentially increase a young saguaro's chance of survival (Drezner, 2004). In fact, saguaros possess fleshy red fruits (Kearney and Peebles, 1960; Hickman, 1993) that are consumed and dispersed by animals to shaded areas under potential nurse trees and shrubs (van der Pijl, 1982; Bregman, 1988).

Saguaro regeneration is episodic, occurring only during climatically favorable years that include ample summer and pre-monsoon rainfall and absence of extreme freezes (Brum, 1973; Steenbergh and Lowe, 1976; Jordan and Nobel, 1982; Turner, 1990; Pierson and Turner, 1998). Various studies have attempted to link regeneration with pollution (Stolte, 1992), rodent digging and herbivory (Niering et al., 1963; Steenbergh and Lowe, 1969), El Niño (Drezner and Balling, 2002), and even bacterial necrosis associated with saguaro decay (Alcorn, 1959–1960; Alcorn and May, 1962). Nonetheless, saguaro populations are primarily controlled by climate (Steenbergh and Lowe, 1977), and the species cannot successfully regenerate without the benefits of a nurse (Turner et al., 1966).

Nurse associations are dynamic over both space and time, and influence the entire Sonoran Desert ecosystem (McAuliffe, 1988). At the community scale, saguaros are found disproportionately more often under nurse plants than expected relative to nurse cover in Organ Pipe Cactus National Monument (OPCNM), due either to directed dispersal by animals to shade (Hutto et al., 1986; Turner et al., 1995) or more likely, differential survivorship (Turner et al., 1966). Parker (1989) and

Hutto et al. (1986) observed that saguaros were found less often than expected under the open-canopied *Larrea tridentata* (DC.) Coville (Fig. 1(d)) at OPCNM. Brum (1973) noted that saguaros in marginal populations were associated disproportionately more often with *Cercidium microphyllum* (Torr.) Rose and Johnston (a leguminous tree, Fig. 1(c)) than with other nurse species, leading him to suggest (though Brum did not test) that perhaps this species was a superior nurse. *Cercidium microphyllum* moderates extreme temperatures better than the dense shrub *Ambrosia deltoidea* (Torr.) Payne and daytime high temperatures are more uniform under the canopy of *C. microphyllum* (Drezner and Garrity, 2003; Fig. 1).
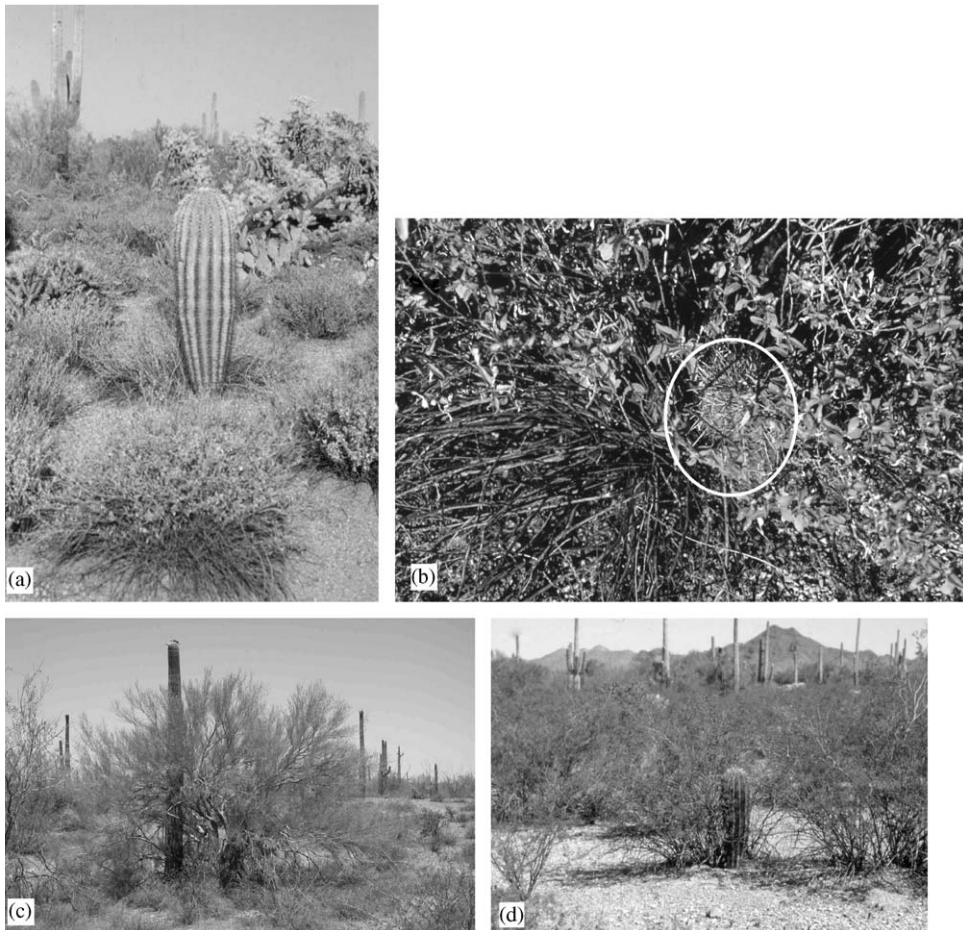

Fig. 1. Saguaros and their nurses. (a) Saguaro with *Ambrosia deltoidea* (photo from the Usery Mountains near Mesa, Arizona); (b) a young saguaro under *A. deltoidea* (same locale as (a)). The saguaro can be identified by locating its spines just inside the circle in the 8–11 o'clock positions. Saguaro associated with the tree *Cercidium microphyllum* is shown in (c), in Organ Pipe Cactus National Monument; (d) saguaro associated with *Larrea tridentata* in Organ Pipe Cactus National Monument. All images taken by author.

Perhaps the only mention of saguaro subcanopy patterns was made by Franco and Nobel (1989) as part of a larger study. They noted that 25 saguaro seedlings in OPCNM under *A. deltoidea* (Fig. 1) were clustered near the base of the nurse, though they did not analyze the clustering statistically. They related this to differences in soil surface temperatures under a nurse's canopy and in the open (Franco and Nobel, 1989). Subcanopy conditions are not even. For example, insolation receipt decreases towards the base (Castellanos et al., 1999). Different nurses with canopies of varying size and density will create different kinds of microhabitats beneath their canopies. Leaf and canopy density likely influence other microclimate conditions as variations in structure reflect differences in shading, insolation and other microenvironmental conditions.

Withgott (2000) and Callaway (1995) argue that ecologists typically focus on competition and negative plant interactions, but only recently have nurse associations and positive plant interactions been considered more carefully, in a new and burgeoning area of ecological research. The close proximity of different species and how they influence each other in a climatically harsh environment require further exploration (Withgott, 2000). The present study will contribute to the important and growing interest in nurse associations and positive species associations, as called for by Withgott (2000, p. 484) in *BioScience*, "…the new developments in the ways people view nurse effects promise to yield further progress and provide a more balanced understanding of how natural systems function."

In order to understand the benefits derived by saguaro cacti from their nurses, fundamental questions must be asked. For the first time, the present study will quantify and statistically analyze the distributional patterns of saguaro–nurse associations at their scale of interaction, the subcanopy scale, using a dataset from 30 locations throughout 50,000 km^2 of the Sonoran Desert. I test three hypotheses: (1) Saguaros are distributed disproportionately more often near their nurse's base than at their nurse's periphery. (2) Saguaro distribution (extent of clumping) under their nurses will vary with nurse canopy type and architecture. (3) Saguaros will be associated with some nurse types (based on canopy structure) more than with others than expected by chance.

2. Methods

2.1. Study site

The study was conducted over most of the saguaro's range in the United States. An area of more than 50,000 km^2 was sampled, from about 31.89° to 33.86°N latitude and 110.72° to 114.30°W longitude (Fig. 2). Saguaro populations sampled are part of the Lower Colorado River Valley and Arizona Upland subdivisions of the Sonoran Desert (Shreve, 1951; Turner and Brown, 1994). The Sonoran Desert is characterized by two distinct seasons of rainfall. During the summer months, the summer monsoon brings moisture from the Gulfs of Mexico and California (Carleton, 1986). Convectively generated thunderstorms develop locally (Carleton,
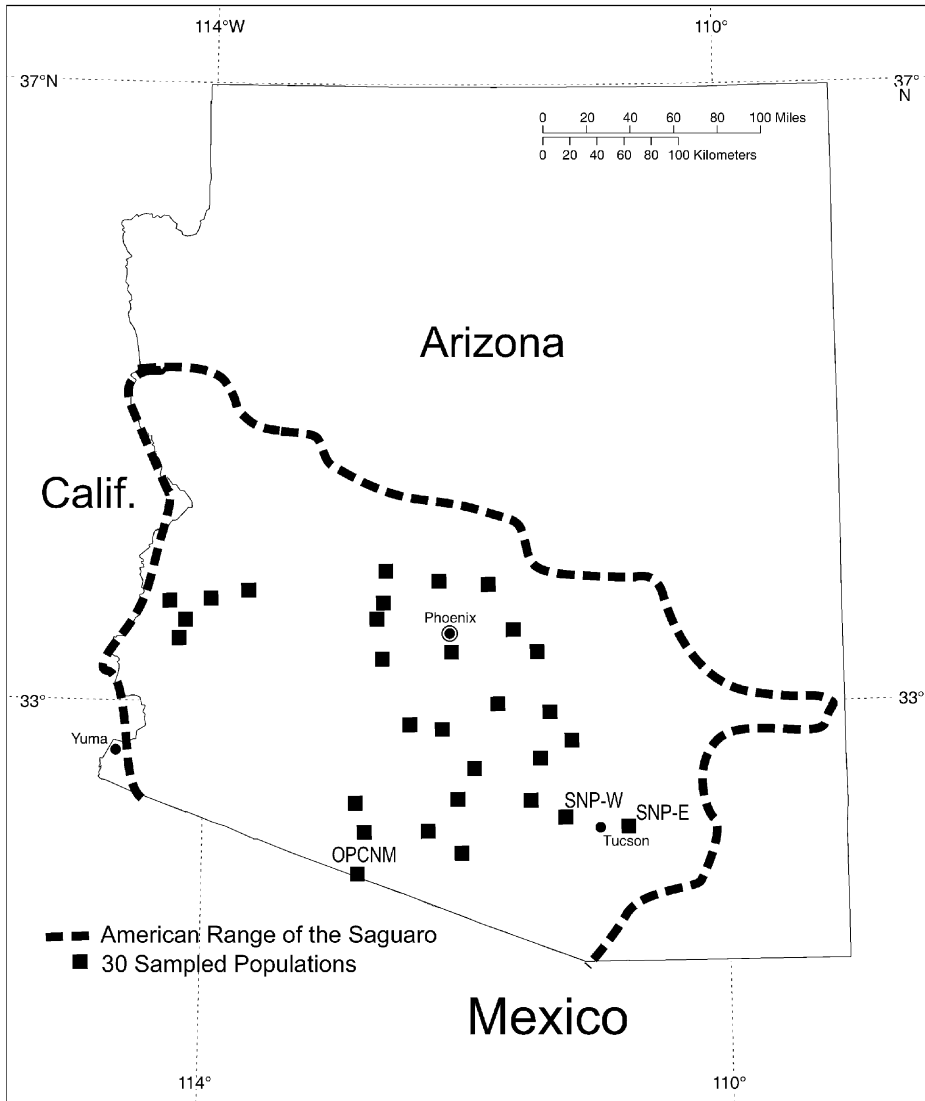
Fig. 2. Map of 30 saguaro populations sampled and location of Saguaro National Park (SNP) East and West, and Organ Pipe Cactus National Monument (OPCNM). Saguaro range modified from Turner et al. (1995).

1987). Thirty-year rainfall averages for June to August are about 4.5 cm in the Tucson area to about 1–1.5 cm in the western plots (Drezner, 2003a). During the winter, extra-tropical cyclones bring frontally induced regional rainfall (e.g. Hastings and Turner, 1965), ranging from 7 to 8 + cm in the northeast to about 4 cm or less in the west (Drezner, 2003a). Summer temperatures regularly exceed 40 °C, and may occasionally drop below freezing during the winter, the frequency varying by

location. El Niño also influences the Sonoran Desert climate (Ropelewski and Halpert, 1987; Andrade and Sellers, 1988; Sheppard et al., 2002) including increased cold season precipitation (Woodhouse, 1997). In addition to the six common nurse species considered in this study, other species observed over the study sites include *Fouquieria splendens*, *Encelia farinosa*, *Krameria* spp., and the cacti *Opuntia* spp. and *Ferocactus* spp.

2.2. Field methods

Thirty populations were sampled. Plots were located based on several criteria. In all but three cases, plots were more than 20 km from the nearest plot, and the two closest plots were 13 km apart. For control, plots were flat (most plots less than 3% slope, see Yeaton and Cody, 1979), and washes were avoided and excluded (e.g. Drezner, 2003a). Fifteen to 21 saguaros were quota sampled in each plot (e.g. Brum, 1973), depending on density; plot size varied from less than 400 to over 11,000 m^2. Data were collected on nurse association, nurse canopy diameter, total nurse species cover in the plot, distance and compass direction from the base of the nurse to the center of the saguaro, and location of plots (using GPS) ($n = 537$). Vegetation cover was sampled using a plotless sampling technique (Mueller-Dombois and Ellenberg, 1974; Drezner, 2003b). Because *Ambrosia deltoidea* and *A. dumosa* (A. Gray) Payne individuals may establish near already established saguaros and because of their short life-span (Hutto et al., 1986), *Ambrosia* individuals associated with saguaros more than $\frac{1}{2}$ m in height were excluded when *Ambrosia* spp. was the associated species, as they were probably not the saguaro's nurse. All saguaros associated with the other longer-lived nurse species were included. Of the saguaros sampled, 247 were associated with common nurse plants (*A. deltoidea* ($n = 44$, Asteraceae, shrub), *A. dumosa* ($n = 4$, Asteraceae, shrub), *Cercidium microphyllum* ($n = 87$, Fabaceae, tree), *Larrea tridentata* ($n = 59$, Zygophyllaceae, shrub), *Olneya tesota* ($n = 37$, Fabaceae, tree), *Prosopis* spp. ($n = 16$, Fabaceae, tree)) and were the focus of the present study. Several additional saguaros were associated with less common species, but due to small sample sizes and large variations in canopy architecture, were not included.

2.3. Statistical methods

Nurses were grouped based on size and canopy architecture into three groups: (1) leguminous (Fabaceae) trees (*Cercidium microphyllum*, *Olneya tesota*, *Prosopis* spp.) ($n = 140$), typically several meters in diameter and fairly dense canopies though this varies (this group is referred to as 'trees' in the remainder of the paper), (2) the small, dense canopied *Ambrosia* spp. ($n = 48$) shrubs typically about 1 m in diameter, and (3) the larger and more open-canopied shrub, *L. tridentata* ($n = 59$) (Fig. 1). While canopy density data are not presented in this study, the three structural nurse groups are quite distinct architecturally. Others have similarly observed, for example, the highly sparse canopy of *L. tridentata* relative to, for example, *C. microphyllum* and *A. deltoidea* (Parker, 1989).

Saguaro distance from nurse (base) was standardized to a percent by dividing distance from nurse by nurse canopy radius. For example, if a saguaro was 1 m from the base of its nurse whose canopy radius was 3 m, this saguaro's distance was 33%. All distances discussed in the remainder of this paper refer to this standardized distance. First, average distance and variance were calculated for each of the three nurse groups. Next, a one-way ANOVA was conducted with a post hoc Tukey HSD test for the standardized distances to compare distance to base between the nurse groups. Third, I conducted χ^2 analyses to compare distributional frequencies of saguaros near (inside half) and far (outer half) from base of their nurse, done first by area and then by distance. This was done to observe if there is a non-random pattern, for each nurse type.

Parker (1989) and Hutto et al. (1986) considered whether saguaros were preferentially associated with some species over others in OPCNM. I test this for the saguaros over the combined 30 populations, while controlling for 'false' nurse associations. Specifically, since *Ambrosia* spp. are short-lived and frequently establish near saguaros, I only considered saguaros that were up to $\frac{1}{2}$ m in height that were associated with the common nurse species. For this analysis only, for the purpose of consistency, I only used saguaros up to $\frac{1}{2}$ m in height for the other nurse species as well (total $n = 84$). For each plot, the total cover for each nurse type was divided by the total cover in the plot, and the result was multiplied by the total number of saguaros ($<\frac{1}{2}$ m) in the plot to get the number of saguaros that would be expected to be associated with each nurse type (if saguaro associations are proportional to nurse cover). The expected number of saguaros associated with each nurse type was summed for all plots, yielding the total expected number of saguaros. By calculating the expected proportion of nursed saguaros by each nurse type for each plot individually, the differences in cover over the 30 plots of the different nurse species are directly accounted for in the calculation. χ^2 analysis comparing expected and observed number of saguaros was run to test the significance of the findings. The ratio of observed to expected was calculated, creating an association index that represents whether saguaros are associated more or less than expected with different nurses, which automatically adjusts for species cover in each locale.

Finally, to test whether there is a directional bias in the data, I conducted the Rayleigh test (Batschelet, 1981). This was followed by a second circular statistic technique, the *V* test, which identifies whether the clustering occurs around a given angle (Batschelet, 1981). Thus, the test was repeated 360 times (once for each angle).

3. Results

One-way ANOVA shows that distances are significantly different between the three groups ($p < 0.001$) and the post hoc Tukey test shows that saguaros associated with *L. tridentata* nurses are significantly closer to their nurses' base than saguaros associated with either tree or *Ambrosia* spp. nurses (Table 1). The six χ^2 analyses show that saguaros are found significantly ($p < 0.001$) more frequently under the inside half of their nurse's canopy than the outer half, both by area and distance

Table 1

One-way ANOVA and post hoc Tukey test comparing distances of nursed saguaros from the base of their nurse for *Ambrosia* spp., *Larrea tridentata* and leguminous tree nurses

One-way ANOVA ($p<0.001$) Nurse	n	Average	Variance	Std Error
Larrea tridentata	59	0.241	0.023	0.020
Ambrosia spp.	48	0.333	0.025	0.023
Trees	140	0.382	0.044	0.018
Post hoc Tukey Test	Sig.			
Larrea tridentata-trees	<0.001			
Larrea tridentata-*Ambrosia*	<0.05			
Ambrosia-trees	—			

Distance values are standardized as percentages for each saguaro and nurse (distance from nurse base/ canopy radius). The average distance from the base of the nurse for each nurse group is provided as well as the standard error. For example, the 48 saguaros under *Ambrosia* nurses were, on average, $\frac{1}{3}$ of the distance to the canopy edge from the base.

Table 2

Frequency of individuals on the inside half of the canopy and the outside half for *Ambrosia* spp., leguminous trees (further broken down in the lower half of the table; *C. microphyllum = Cercidium microphyllum*), and for *Larrea tridentata*

	Area relative to canopy			Distance relative to canopy		
	$<\frac{1}{2}$ area	$>\frac{1}{2}$ area	Sig.	$<\frac{1}{2}$ radius	$>\frac{1}{2}$ radius	Sig.
Larrea tridentata	58 (98%)	1 (2%)	<0.001	53 (90%)	6 (10%)	<0.001
Ambrosia spp.	47 (98%)	1 (2%)	<0.001	42 (88%)	6 (13%)	<0.001
Trees	128 (91%)	12 (9%)	<0.001	105 (75%)	35 (25%)	<0.001
C. microphyllum	81 (93%)	6 (7%)	<0.001	66 (76%)	21 (24%)	<0.001
Olneya tesota	35 (95%)	2 (5%)	<0.001	30 (81%)	7 (19%)	<0.001
Prosopis spp.	12 (75%)	4 (25%)	<0.05	9 (56%)	7 (44%)	—

Significance for χ^2 analyses. Values and significance levels are also provided for frequency of individuals within $\frac{1}{2}$ of the distance to base of nurse (representing $\frac{1}{4}$ of the area) from edge of canopy and more than $\frac{1}{2}$ the distance.

from stem/trunk. Because this analysis assumes that expected frequencies in each cell are equal, more than and less than $\frac{1}{2}$ the nurse canopy's radius is not an ideal test because the area under cover within $\frac{1}{2}$ the radius represents only $\frac{1}{4}$ of the area available to a saguaro. Thus, one would expect 75% of the saguaros to be located under the outer portions of nurses' canopies in the $\frac{1}{2}$ radius test if the saguaros were evenly distributed beneath their nurse's canopy. However, the results are noteworthy and are provided for reference (Table 2).

The observed clustering is illustrated in Fig. 3, demonstrating the tightest clustering around *L. tridentata* and the least basal clustering around tree nurses.
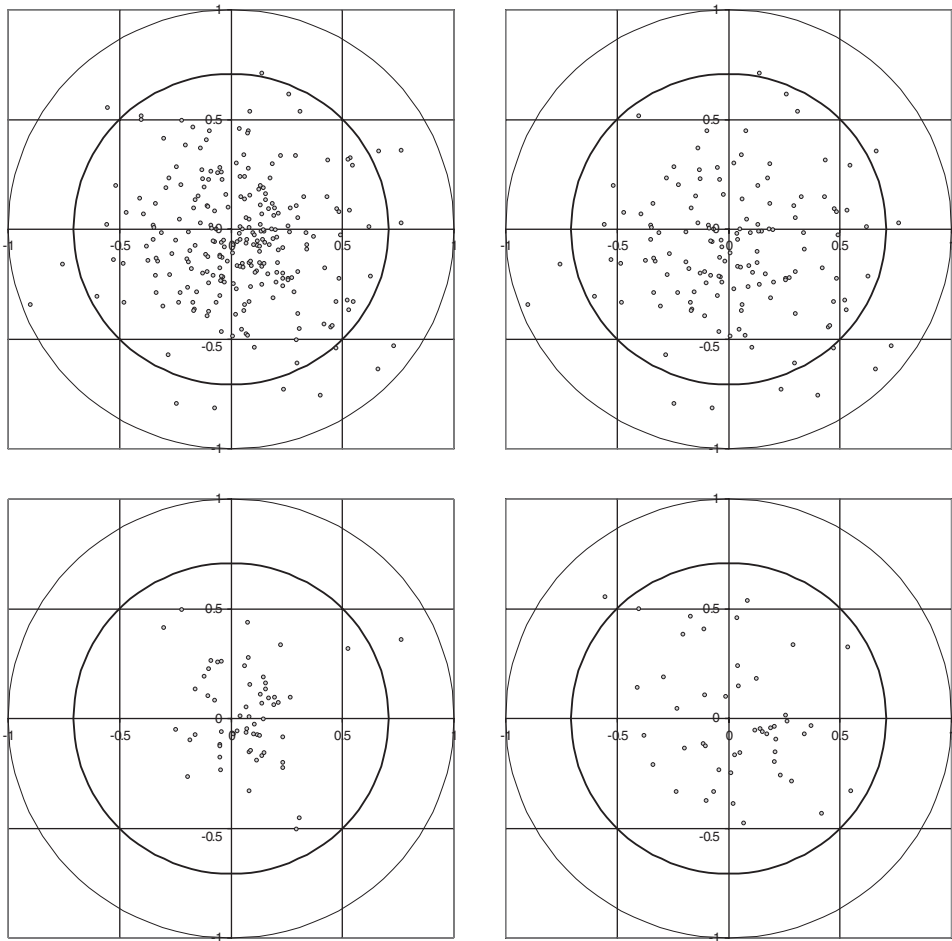
Fig. 3. Distribution of saguaros under nurse plants. Each point represents a saguaro under a statistically standardized nurse, its location calculated based on its % linear distance between trunk/base and edge of canopy. Top left: all nurses ($n = 247$); top right, tree nurses ($n = 140$); bottom left, *Larrea tridentata* nurses ($n = 59$); bottom right, *Ambrosia deltoidea* and *A. dumosa* nurses ($n = 48$). The outer circle represents the edge of the canopy. The inner circle delineates the inside and outside half (area) of the nurse's canopy cover. North is towards the top of the page in all four figures.

Fig. 4 depicts the percent of individuals in each group found in concentric 10% area circles (i.e. each ring covers 10% of the area beneath a standardized nurse canopy), clearly showing the clustered distribution near each nurse's base. Over 81% of saguaros under *L. tridentata* are located within the inner 10% of the area beneath the nurse's canopy, whereas only half of saguaros under *Ambrosia* spp. and 43% of saguaros under trees are located within the inner 10% of the area beneath the nurse's canopy (Fig. 4).
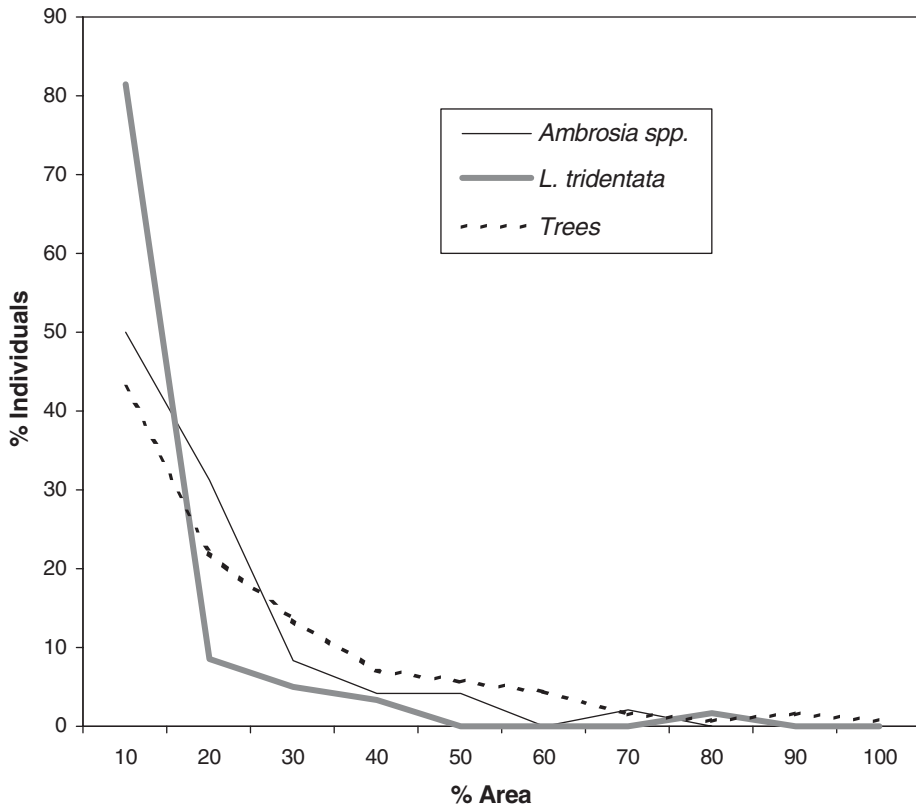
Fig. 4. Percent of saguaros (per nurse group), found in 10% area intervals (*x*-axis). The inside 10% of subcanopy cover supports the highest percent of individuals, the next 10% area ring, the second highest percent of individuals etc. If saguaros were randomly distributed, all three curves would be horizontal lines at 10%.

The χ^2 analysis on the association index is significant ($p < 0.001$) (Table 3). *Ambrosia* spp. have the highest ratio. Of the 84 saguaros under $\frac{1}{2}$ m in height that were considered, about 30 should have been associated with *Ambrosia* spp. based on its cover over the area studied. However, 48 saguaros were associated with this nurse. Trees were represented approximately as expected based on their cover. Nearly 27 saguaros should have been associated with *L. tridentata*, yet only 11 were observed (Table 3).

Finally, the Rayleigh test results demonstrate that a statistically significant bias exists in the distribution of the 247 saguaros around their nurses ($p < 0.001$). The *V* test results for all 360° indicate that the bias is to the south and east. A significant bias ($p < 0.05$) was observed in all angles between (and including) 73° and 209°. The lowest *p*-value (most significant) was obtained for 141° ($p < 0.001$), 6° south of southeast.

Table 3
Expected and observed associations of saguaros up to $\frac{1}{2}$ m in height ($n = 84$)

	Ambrosia spp.	Trees	*Larrea tridentata*
Expected ♯ of saguaros	29.9	27.5	26.6
Observed ♯ of saguaros	48	25	11
Ratio (observed/expected)	1.61	0.91	0.41

For each plot, total cover for each nurse type was divided by the total cover, and the result was multiplied by the total number of saguaros. Thus, the expected number of saguaros is the total number of saguaros expected to be associated with that nurse based on the nurse's cover in the 30 plots. The ratio of actual (observed) to expected number of saguaros for each nurse type was calculated creating an association index. For example, based on its cover, *Ambrosia* spp. would be expected to nurse about 30 of the 84 saguaros, but it actually nurses 48 saguaros. The goodness-of-fit χ^2 result for the three (combined) expected and observed values is significant ($p < 0.001$).

4. Discussion

Saguaro seedlings may only be 3 mm tall by the end of their first year (Steenbergh and Lowe, 1983; Drezner, 2003c). As a result, many saguaros perish from freezing winter temperatures (Nobel, 1980a) and from desiccation in the summer when only saguaros under a nurse survive (Turner et al., 1966). Saguaro distribution patterns under their nurses reflect the influence of many environmental factors; however, survival patterns are strongly linked to climate, and thus to nurse canopy structure, as climate ultimately limits the species (Steenbergh and Lowe, 1977, 1983; Nobel, 1980b).

For all three nurse groups, the small, relatively dense, leafy shrubs *A. deltoidea* and *A. dumosa* (= *Ambrosia* spp.), the larger open-canopied *L. tridentata* (Fig. 1(d)) shrubs, and the large leguminous trees (*C. microphyllum, O. tesota, Prosopis* spp.), saguaros were distributed significantly closer to the base of their nurse relative to the canopy periphery over the 30 populations. Other cacti are also distributed disproportionately closer to their nurses' bases (Valiente-Banuet et al., 1991). Saguaros associated with *L. tridentata* were significantly more clustered than the other two nurse groups. The greater number of saguaros at the periphery of tree canopies relative to *Ambrosia* and *L. tridentata* canopies likely reflects the more spatially consistent subcanopy temperatures found under *C. microphyllum,* and more moderate (both daytime high and night-time low) temperatures found under this tree than beneath *A. deltoidea* (Castellanos et al., 1999; Drezner and Garrity, 2003; Fig. 1).

Over the 30 populations, the association index (proportion of saguaros associated with a nurse relative to that nurse's cover) is higher for *Ambrosia* than for trees, with *L. tridentata* being the lowest. Parker (1989) and Hutto et al. (1986) found fewer saguaros associated with *L. tridentata* and *Fouquieria splendens* (highly open-canopied) than expected in OPCNM. They suggest that this may be due to microclimatic differences, though they do not rule out seed dispersal (e.g. Simons and Simons, 1993; Bullock and Moy, 2004), seed predation or poor soils as possible

causes (Hutto et al., 1986; Parker, 1989). Empirical tests show that none of 1200 unshaded saguaro seedlings survived their first year of life, while 35% of 1200 shaded seedlings did survive (Turner et al., 1966). Saguaros are also disproportionately (significantly) distributed beneath the warmer south side of their nurse in colder parts of their range; however, this trend is not observed in warmer regions (Drezner and Garrity, 2003), further indicating that climate is important at this scale. Perhaps in the warmest parts of their range there may be a northern or no bias, but this has not been tested. *Coryphantha pallida* is distributed to the north and west of its nurse in the southern part of the North American deserts (Valiente-Banuet et al., 1991). Daytime high and night-time low temperatures under *C. microphyllum* were more moderate than under *A. deltoidea* (Drezner and Garrity, 2003). Simply because of nurse height and life-span, a *C. microphyllum* nurse will affect its saguaro nursee longer than *A. deltoidea*; however, a saguaro may not derive as much benefit from its nurse after its first few years of life (e.g. Turner et al., 1995). The present study used circular statistics to confirm a south to southeasterly bias in the distribution of saguaros under their nurses. It seems unlikely that seed dispersal, predation or variable soil would result in a southerly distributional bias over the tens of thousands of square kilometers sampled (involving several different nurse species). Nurses also extend the saguaro's range northward by reducing night-time winter heat loss and by maintaining elevated night-time temperatures beneath their canopy (Nobel, 1980a). The size and extent of suitable areas for a nursed species depend on the characteristics of the nurse, and final subcanopy distributional patterns will be associated with nurse canopy characteristics.

Steenbergh and Lowe (1977) suggested (though did not test) that the more frequent distribution of saguaros beneath their nurse is due to greater seed dispersal to these locales coupled with greater seed predation in the open (e.g. also Olin et al., 1989). Hutto et al. (1986) revisit this question, sampling soil beneath *C. microphyllum* canopies to quantify saguaro seed presence. They did not test subcanopy clumping, only association with a nurse. They sampled soil at the subcanopy radius midpoint and at the canopy edge, and obtained a seed presence ratio of 4.6:1 (Hutto et al., 1986). In the present study, I compared the middle 10% subcanopy area with the 10% area under the canopy's edge (data not shown). For *C. microphyllum*, the ratio was 14:1, and for all trees, 20:1, even with the relatively even distribution of saguaros under *Prosopis* (Table 2). Thus, while there are 4.6 times as many seeds under the canopy midpoint than at its edge, I observed 14 times as many saguaros there. While these samples are too small to draw conclusions, they do indicate that seed dispersal and predation alone may not account for the clustered patterns observed. Irrespective of the possible causes (which are almost certainly a combination of many factors and not the outcome of one), I observed a clear and significant pattern of association (and preferential clustering) between saguaros and their nurses in a combined dataset from 30 locales over the northern Sonoran Desert.

Subcanopy cover is typically densest near the base, and decreases outward towards the canopy edge. Castellanos et al. (1999) demonstrated that the canopy of *C. microphyllum* exhibits a horizontal gradient in light from the base of the trunk outwards in the Sonoran Desert and vines exploit such differences in subcanopy

microhabitat. Differences in canopy structure must almost certainly create variable environmental and climate conditions in the subcanopy. Future work should specifically quantify differences in subcanopy microclimate conditions and how this influences saguaro survivorship directly. Canopy structure (e.g. leaf size and density of canopy) likely influences soil surface temperatures, amount of photosynthetically active radiation (PAR) receipt, air temperature and possibly humidity. In addition, soil moisture may be a factor; Kropfl et al. (2002) found reduced soil moisture beneath *L. divaricata* (closely related to *L. tridentata*) canopies than in the open. In addition, throughfall by stems may vary across species (Abrahams et al., 2003). I expect the very open-canopied *L. tridentata* to provide the best conditions in the most densely covered subcanopy areas near its base, while the large, dense leguminous trees provide suitable conditions under a larger portion of their canopies. The findings confirm this, as few saguaros establish far from *L. tridentata*'s base, while saguaros are found under a larger portion of tree subcanopies.

Subcanopy temperature and microclimate have similarly been quantified beneath nurses demonstrating the more moderate conditions found in the subcanopy environment (Lowe and Hinds, 1971; Dawson, 1993) and benefits are documented (e.g. Evans et al., 1994; Callaway, 1995; Whitford, 2002). Some disadvantages may also be observed, such as light reduction (Holmgren et al., 1997) and reduced soil moisture due partly from canopy interception, as observed in *L. divaricata* (Kropfl et al., 2002). In less extreme environments, competition likely dominates plant relations, while under harsher environmental conditions, facilitation may be more important (Bertness and Callaway, 1994; Holmgren et al., 1997). Holmgren et al. (1997) suggest that the nursed plants derive moisture benefits from establishing under another plant's canopy, but must pay the cost of reduced light. Under extreme conditions such as arid environments, the water benefits outweigh the costs, which is not necessarily true in a less extreme environment (Holmgren et al., 1997; Whitford, 2002).

The growing attention to plant interactions and nurse associations reflects our growing understanding of ecosystem function, and of the interrelationships and dependencies found between different species (Callaway, 1995; Withgott, 2000). This is the first study to quantify and statistically analyze the spatial relationships between saguaros and their nurses, as well as to compare patterns under different nurses with different canopy architectures. In fact, it is precisely at the poorly explored subcanopy scale that direct interactions occur and benefits are derived. I relate findings to the regional scale. While there may be other reasons why saguaros establish disproportionately more often under *Ambrosia*, such as being better hidden from animals, secondary microenvironmental benefits like reduced soil surface temperatures (Franco and Nobel, 1989) or other reasons not considered in this study, I suggest the reason for the observed saguaro distributions is that nurse species that impart greater microenvironmental benefits, which may include increasing shade, reducing the summertime radiation load, increasing night-time winter temperatures, increasing soil moisture, and reducing herbivory, thus influence patterns of survival and association across the harsh desert environment where positive plant interactions are often observed.

Acknowledgments

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