

## NESTEDNESS OF REMNANT SONORAN DESERT PLANT COMMUNITIES IN METROPOLITAN PHOENIX, ARIZONA

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**Abstract.** Urbanization can have profound effects on the plant communities persisting in remnant habitats. That process can be explored by examining patterns of nestedness. Species composition for a set of communities exhibits a nested pattern if species present in progressively richer assemblages form a series of subsets. Nestedness can form as a result of the dynamic processes of extinction or colonization. It can also reflect a nested distribution of habitats among the sites or the differential abundance properties of species through passive sampling. This study investigated whether Sonoran Desert woody vegetation in remnant islands within metropolitan Phoenix is nested and explored which mechanisms are responsible for the pattern. It also examined whether vegetation is nested in similar habitat types across islands, and how species abundance relates to the nested pattern and hypothesized mechanisms. All data sets were significantly nested, indicating a nested pattern at the island and habitat levels. Community-level analyses did not indicate a primary mechanism leading to the nested pattern. Among species with abundances correlated with the nested rank-order of sites, abundance properties were significantly related to different variables. This suggests that individual taxa respond to divergent ecological mechanisms, leading to nestedness. Thus, nestedness in plant communities can result from a complex set of contributors and may not be attributable to a single factor.

**Key words:** *Arizona; CAP (Central Arizona-Phoenix)-LTER; nestedness; plant community; Sonoran Desert; urban ecology.*

### INTRODUCTION

Because of the prevalence of land development and landscape change, natural habitats often consist of discrete, disconnected remnants surrounded by an inhospitable matrix. Understanding the patterns and processes responsible for community composition in fragmented landscapes is an important goal of resource conservation and ecological theory. Studying community composition, in which attention is paid to species identities, illuminates system features unapparent to analyses of richness alone. Richness data can reveal that species have been lost, but often one must examine composition data to know how or why a system loses species. Nestedness analysis can potentially indicate which mechanisms structure communities and whether certain species in a fragmented system are likely to colonize new areas or face extinction. This study considered whether vegetation on desert habitat islands embedded within the urban matrix of the Phoenix metropolitan area, locus of the Central Arizona-Phoenix Long Term Ecological Research (CAP-LTER) site, exhibits a nested pattern, and what mechanisms may be responsible for that pattern.

### *Nestedness theory*

A data set exhibits a nested pattern if species found in progressively richer assemblages form a series of subsets (Patterson 1987, Atmar and Patterson 1993). Perfect nestedness means that all species observed in depauperate sites will be found in all richer locations. While perfect nestedness is very rare in nature, the degree of nestedness can be measured and significance assessed using simulations based on null models. Nestedness requires three conditions: species possess a shared biogeographic history, habitats are somewhat comparable, and species are hierarchical in distribution and frequency (Patterson and Brown 1991). Since nestedness refers to a condition of ordered composition, any factor that serves to create heterogeneity will reduce the propensity for nestedness (Mikkelsen 1993, Wright et al. 1998). As such, the first two conditions serve as homogeneity constraints on species and sites, respectively; the third condition acts as a filter and reflects the factors that lead species to have variable incidences (Wright et al. 1998).

Several mechanisms can cause nestedness (Patterson 1987, Cutler 1994, Cook and Quinn 1995, Wright et al. 1998). Darlington (1957) was the first to recognize a nested pattern among oceanic archipelagos and attributed this to the differential colonization of islands by species. Since dispersal abilities differ among species,

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more isolated islands would only contain those taxa capable of long-distance dispersal over the ocean or an otherwise inhospitable matrix. Extinction of species could also produce nested communities if vulnerability to population collapse differs among species. The area of available habitat acts to constrain population size by dictating an approximate maximum number of individuals capable of being supported on an island (Preston 1962). Small populations tend to be more vulnerable to stochastic extinction events (MacArthur and Wilson 1967, Gilpin and Soulé 1986, Fischer and Stöcklin 1997, Menges and Dolan 1998, Gray et al. 2003, Matthies et al. 2004).

While colonization and extinction imply the dynamic processes of assembly and disassembly, nestedness can reflect other underlying ecological patterns. Sites differing in habitat heterogeneity can form nested subsets if less common habitats support taxa specific to those habitats (Worthen 1996). Thus, sites containing common and rare habitat types may contain both habitat generalists and specialists, while more homogeneous sites would only contain generalist species. Finally, when species consistently differ in their relative commonness and rarity without regard to habitat (Preston 1962), they can form nested assemblages, since common species simply have a higher probability of occupying any given site via passive sampling (Connor and McCoy 1979). These potential mechanisms are probabilistic filters (Wright et al. 1998): habitat nestedness acts to filter habitats, passive sampling is an abundance filter, and isolation and area filters reflect the tendencies for species to differ in their colonization or extinction behavior, respectively. Circumstances over space and time determine whether one or more filters will produce a consistent ordering of species across sites and a nested structure.

The difficulty is how to distinguish which of those filters are primarily responsible for an observed nestedness pattern. The ecological context of an archipelago can be considered as a simple *a priori* indication of which dynamic process is potentially operating. Archipelagos representing contracted remnants of a formerly continuous environment supporting shared species, such as land bridge islands and fragmented landscapes, should develop a nested pattern resulting from differential extinction rates between taxa (Patterson 1987). On the other hand, oceanic islands formed in isolation from other land masses should exhibit nestedness primarily as a result of colonization (Cook and Quinn 1995). While some studies have demonstrated colonization as a driving mechanism (e.g., Kadmon 1995, Butaye et al. 2001, Loo et al. 2002), extinction has more often been indicated (Wright et al. 1998).

Multiple conjectures have been made about how nestedness scores or matrix arrangements can distinguish among these mechanisms (Patterson and Atmar 1986, Patterson 1987, 1990, Cutler 1991, 1994, Wright and Reeves 1992). However, there is no strong

indication, whether through theoretical deduction or empirical demonstration, that different mechanisms would produce fundamentally different nestedness scores (Simberloff and Martin 1991). A more promising approach is to analyze the rank-order correlations between the nested order of sites and candidate independent variables (Lomolino 1996, Patterson et al. 1996, Sfenthourakis et al. 1999, Rodríguez-Gironés and Santamaría 2006). Significant correlations between the nested order of sites and isolation distance or area could indicate the influence of colonization and extinction, respectively, under two fundamental assumptions of island biogeography theory (MacArthur and Wilson 1967): extinction probability declines with increasing area, and the likelihood of immigration decreases with greater isolation (Lomolino 1996).

However, because island area would affect the total number of individuals present, evidence of an area effect could result from either stochastic extinction of smaller populations or the passive sampling of progressively rarer species in larger collections of individuals (Coleman 1981, Coleman et al. 1982, Scheiner 2003). Evidence of an area effect alone cannot disentangle extinction from passive sampling. The most convincing evidence of extinction at the island level would arise from the demonstration of declines in species richness or the loss of specific taxa over time; such evidence is not available for this study. Thus, we cannot distinguish between extinction and passive sampling with these data.

Habitat diversity is potentially an important driver of nestedness (e.g., Honnay et al. 1999, Myklestad and Sætersdal 2004). This relationship is strengthened when at least some species have specific habitat affinities. Significant correlations between habitat heterogeneity and nestedness indicate that the presence of multiple habitat types increases the chance of encountering species not present in more homogeneous sites.

Elevation has a strong effect on the composition of Sonoran Desert vegetation with greater species richness and vegetative ground cover at higher altitudes (Yang and Lowe 1956, Barbour 1973, Halvorson and Patten 1974, Phillips and MacMahon 1978, Bowers and Lowe 1986). Increases in elevation within this study area are accompanied by an increase in mean particle size in the rockier soils on mountains and hilltops, which retards evaporation and promotes deeper percolation of rain water (Shreve and Wiggins 1964), resulting in greater water availability to plants. Thus, elevation is a surrogate for productivity. Higher productivity can result in a greater density of individuals, which can passively sample more species. Also, multiple woody species that thrive at higher altitudes are not observed on lower slopes and plains due to moisture limitation. Hence, sites with wider ranges in elevation potentially offer a broader productivity gradient and an increase in island species richness.

### *Aims of the study*

Given the widespread distribution and substantial influence of human-dominated landscapes on surrounding ecosystems, understanding how cities affect biota is now recognized as an important goal in ecology (Rebele 1994, Grimm et al. 2000, Grimm and Redman 2004). Urban systems also offer a valuable context in which to study phenomena that have concerned ecologists for decades, such as how habitat fragmentation affects community composition. Nestedness analysis offers a useful means by which to assess how composition is structured. This study determined whether nestedness exists for woody vegetation among remnant islands in the Phoenix metropolitan area, and what mechanisms may be responsible for the nested pattern. While there has been an increase in attention paid to nestedness in plants, no studies have yet examined this pattern in an urban environment.

This study is also unique in investigating whether nestedness is evident within similar habitat types across different islands. The analysis indicates whether the nested pattern is independent of habitat heterogeneity, thereby implicating other mechanisms, and whether nestedness is a hierarchically scaled pattern detectable at smaller scales than entire bounded islands. Owing to habitat affinities, there should be smaller assemblages of species in each habitat than are found on entire islands; it is not known how such a limitation will affect nestedness.

In addition, the recording of species abundance allowed for an independent test and potentially greater resolution on mechanisms contributing to nestedness. These mechanisms may act on the abundance characteristics of individual species. If different species react to a common mechanism, it lends support to that particular factor being the primary influence on the nested pattern. On the other hand, if different species respond to divergent mechanisms, this may indicate that multiple determinants combine effects to contribute to nestedness of the community at large. To our knowledge, this study is the first one to explore the relationship between species abundance and community nestedness.

## METHODS

### *Data sampling*

Plant diversity data were recorded in 22 undeveloped remnant islands scattered throughout the Salt River Valley in the Phoenix metropolitan area (Appendix A). All islands consisted of Sonoran Desert habitat, possibly disturbed in the past but never developed, surrounded by residential and commercial land covers. Due to the prevalence of disturbance associated with development, impermeable surfaces, and common planting of nonnative horticultural plants, the intervening urban matrix is exceedingly inhospitable to the migration of native desert plant species. Most patches are mountainous parks dedicated to preserving natural habitat for

recreation and conservation. Mountains in this system rise to a maximum of ~500 m from base to summit, with most substantially lower. Since Phoenix is a relatively new city, becoming urbanized only after World War II, most islands have been isolated for <50 years.

The woody community consisted of a wide variety of shrubs, trees, and cacti, which was sampled between 1998 and 2002. All data were recorded from a system of transects. A transect consisted of five quadrats, each a circle 100 m<sup>2</sup> in area, separated from each other by 20 m edge to edge. The number of woody individuals identified to species was recorded for each quadrat. Species abundance was calculated as the per site mean number of individuals present per 100 square meters. Transects were stratified by geomorphic type, which includes: slopes facing one of the four cardinal directions, flatlands, and ephemeral washes. Within a geomorphic type, the position of the first quadrat and the transect trajectory were determined randomly.

### *Data analysis*

Independent variables describing island properties were calculated with a variety of methods. For use in determining both the effective area and habitat heterogeneity of the study sites, all geomorphic types were mapped using ArcView 3.3 (2002) by tracing polygons over digitized aerial photographs (Kenney Aerial Mapping 2000) taken at ~0.33 m resolution. Polygons were designated to encompass areas containing continuous expanses of the desert environment lacking urban features as barriers. A contour map with 10-m intervals, generated using ArcGIS (2002) and derived from the Maricopa County Digital Elevation Model (DEM; *available online*)<sup>4</sup> was used in conjunction with the aerial photos to aid in interpretation. Reliance on two-dimensional GIS layers alone would distort the relationship between polygons by overemphasizing flatter areas at the expense of steeper slopes. To compensate for this distortion, the three-dimensional surface areas of each polygon were estimated by dividing the two-dimensional area by the cosine of the mean slope for that polygon; the Maricopa DEM was converted into a map of slope values, at 30-m resolution, and the mean was calculated for each polygon.

Effective surface areas for the 22 islands were calculated as the sum of all three-dimensional polygons, excluding major disturbances and recreational facilities. Mean elevation was calculated from the Maricopa DEM values contained within the site boundaries. Habitat heterogeneity maps for the islands were generated by combining the geomorphic-type maps with a layer depicting soil types (Soil Survey Geographic Database 2002). Habitat diversity for each island was calculated using the Shannon index (Magurran 1988), which incorporated the proportion of total surface area

<sup>4</sup> (<http://data.geocomm.com/>)

covered by each geomorphic type–soil class. Isolation was calculated as:  $I = \Sigma [\ln(\text{Area})/(\text{Distance}^2)]$ , where distance extended from the edge of the focal island to the edge of other islands or to the nearest expanse of outlying desert. For this purpose, the area of the outlying desert was assumed to be 9000 ha, which is approximately equal to the area of the largest island, South Mountain Park. The isolation index was intended to express the potential for a given patch to exchange propagules with other source areas and facilitate establishment of new species; this potential decreases with longer distances between sites and increases with larger areas bearing more plants and richer communities of animal vectors.

The total density of individuals for a site was calculated as the mean number of plants per quadrat, regardless of species identity. This provides a means by which to examine whether simply increasing numbers of individuals, apart from other factors, increases species richness so that nestedness is more likely observed. Nestedness is observed when species frequencies are hierarchical; if many species have similar commonness, they will appear as interchangeable in the data, creating a noisier matrix and decreasing the degree of nestedness.

The nestedness of each data set was analyzed using the Nestedness Temperature Calculator (Atmar and Patterson 1993), which yields a nestedness score ranging from 0 to 100. The score 0 denotes perfect nestedness; increasing disorder in the matrix increases the score so that randomly generated matrices generally have temperatures around 70–80. The NTC has been criticized by multiple authors for being overly biased toward finding significant nestedness in field data from the use of unrealistic null matrices, resulting in a higher probability of Type I statistical errors (Cook and Quinn 1998, Brualdi and Sanderson 1999, Jonsson 2001, Fischer and Lindenmayer 2002). Rodríguez-Gironés and Santamaría (2006) created a new algorithm, BINMATNEST, which addresses criticisms of the NTC and uses three different null matrices as described in Atmar and Patterson (1993), Fischer and Lindenmayer (2002), and their own paper. Their program, available as a supplement to their paper, was used in order to compare nestedness scores using different metrics. Spearman rank-order correlations were calculated between the nested rank-order of sites and independent variables. Multiple regression between the nested rank-order of sites and independent variables was utilized to assess the contribution of the factors to the nested pattern.

To investigate whether woody species abundance varies among remnant islands in a manner consistent with nestedness, the relationship between the nested rank-order of sites and individual species abundance was assessed by calculating the Spearman rank-order correlation. A significant positive correlation indicates that species abundance declines in progressively depauperate sites. Nestedness analysis using the NTC and BINMATNEST is based on presence–absence data at

the community level. We hypothesized that species responding to mechanisms structuring nestedness will have dwindling abundance down the gradient until they are ultimately lacking on depauperate islands, reflective of their extinction in less hospitable sites. Alternatively, species may be rare or absent in sites lacking certain environments, leading to nestedness reflective of the availability of growth conditions. Spearman rank-order correlations were also calculated between focal species abundance and independent variables.

For the abundance analysis, a subset of 14 species out of 52 sampled were selected, each belonging to one of the following representative categories: the five most frequent species (at least 19 sites occupied out of 22; group 1), species intermediate in frequency (8–12 sites occupied out of 22) generally following the nested rank-order of sites (group 2), and species intermediate in frequency that did not follow the nested pattern (group 3). Species determined to follow the nested pattern occupied the richer communities occurring higher in the nested rank-order of sites; the latter three species not conforming to the nested pattern had presences and absences dispersed throughout the matrix regardless of the nested rank-order of sites. Six species fit the criteria for group 2. *Prosopis velutina*, present in 13 sites, was analyzed with the two other species in group 3. Thirty-three species were present in fewer than eight sites and were judged to be too infrequent for this analysis.

This study also investigated whether declines in species abundance across sites were evident at the habitat level. For each focal species, the Spearman rank-order correlation was calculated between species abundance and the nested rank-order of sites determined for that habitat in which the species had the highest mean density of individuals per quadrat. The nested rank-order of sites for habitats was obtained from nestedness analysis conducted for vegetation within each habitat type. A significant positive correlation indicated a decrease in species abundance parallel to the nestedness gradient from species-rich to species-poor communities at the habitat level.

## RESULTS

Nestedness was ubiquitous in this system. All data sets tested were significantly nested ( $P = 0.002$  for wash habitat; all other data sets had  $P < 0.001$ ). The flatlands and the north- and south-facing slopes yielded Nestedness Temperature Calculator scores (22.8, 22.4, and 20.9, respectively) comparable to the data set describing the whole islands (22.6). The scores for the east- and west-facing slopes were lower than the islands data set (16.0 and 15.8, respectively), while the score for the washes was higher (31.2). The Pearson correlation between scores from the NTC and BINMATNEST was 0.897. Thus, nestedness for woody species in this system is a hierarchical pattern present at two scales: the entire island and individual habitat types. The size of the

TABLE 1. Multiple regression analysis of the correlation between the nested rank-order of sites and independent variables ( $n = 22$ ,  $R^2 = 0.508$ ).

Independent variable	Standardized coefficient	<i>P</i>
Isolation	0.088	0.614
Habitat heterogeneity	0.455	0.035
Mean elevation	0.451	0.032
Mean density	-0.127	0.728

species pool does not appear to affect the ability of nestedness to form in this system.

Values for independent variables across the nested rank-order of sites, and Spearman correlations between each, are listed in Appendix B. Multiple regression was generally reflective of the Spearman correlations (Table 1). Both mean elevation and habitat heterogeneity were significantly related to the nested rank-order of sites. However, since area is highly correlated with mean elevation and habitat heterogeneity ( $P < 0.01$ ; Table 2), and cannot be included in the same regression, this also indicates a potential area effect contributing to the nested pattern.

Some woody species were less abundant in the depauperate sites (Table 3). Of the 14 focal species, 7 species had significant positive correlations with the nested rank-order of sites. Of these, two are common species and five are of intermediate frequency, generally following the nested rank-order of sites. Though nonsignificant, there are only two species, *Larrea tridentata* and *Prosopis velutina*, negatively correlated with the nested rank-order of sites.

All five independent variables were significantly correlated with between one and seven of the species' abundance rank-orders (Table 3). Only mean elevation was correlated with the same seven species that were also significantly related to the nested rank-order of sites. The other factors were significantly related to four or fewer species. Species abundance for *Larrea tridentata* was negatively correlated with density of individual plants, meaning that this species was more numerous in sparse vegetation. *Larrea tridentata* was the only species significantly related to an independent variable but not to the nested rank-order of sites.

Species abundances of four taxa, all intermediate in frequency and following the nested pattern, significantly decreased down the nested rank-order of sites at the habitat level (Table 4). Habitat type containing peak abundance per species varied between the slope aspects and washes; no focal species reached maximum mean abundance in the flatland habitat. For the three habitats in which the four species achieve peak mean abundance, total area of each habitat within a site was significantly correlated with nested rank-order: north-facing slope (0.458;  $n = 17$ ), east-facing slope (0.534;  $n = 14$ ), and wash (0.763;  $n = 14$ ). The two species with negative

correlations in Table 3, *Larrea tridentata* and *Prosopis velutina*, also had negative relationships in this analysis.

## DISCUSSION

While island area, habitat heterogeneity, and mean elevation are all significantly related to woody species nestedness, Spearman correlations indicate that island area is most highly correlated with nestedness ( $r = 0.87$ ; Appendix B). The area effect is indicative of the influence of extinction or passive sampling, although exactly how the two mechanisms impact the area effect cannot be disentangled with the data available for this study. Distinguishing between the mechanisms requires multitemporal data. For species as long-lived as woody plants in the Sonoran Desert, observing species extinctions resulting from stochastic processes would take many years.

Island area affects the total number of individuals present in a continuous patch of vegetation. Larger islands have more individuals, which allows for larger populations and a lower extinction rate for the remnant vegetation. Alternatively, larger assemblages of individuals have a higher probability of containing progressively rarer species along with common ones, so that larger islands passively sample more species. The total number of individuals is a function of both surface area and the density of individuals. Since mean density does not significantly vary with island area (Table 2), area is the primary determinant of the island's total number of individuals, the community size. Furthermore, because island area is highly correlated with both habitat heterogeneity and mean elevation, it could not be included in the regression analysis. Consequently, the analysis indicated a possible role for four of the five potential mechanisms, excepting only isolation in affecting nestedness.

Analyses of the abundance of particular species across sites provided another means by which to obtain greater resolution on mechanisms contributing to nestedness. The analysis of species abundance at the island level (Table 3) suggests that elevation is an important influence on nestedness. Mean elevation is significantly correlated with each of the seven species also found to be significantly related to nestedness, indicating that sites containing higher elevations also have the highest densities of those species. Three species (*Ephedra*

TABLE 2. Spearman rank-order correlation matrix for independent variables ( $n = 22$ ).

Variable	Isolation	Habitat heterogeneity	Mean elevation	Mean density
Area	0.45*	0.81**	0.62**	0.16
Isolation		0.44*	0.15	0.06
Habitat heterogeneity			0.52*	0.32
Mean elevation				0.46*

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

TABLE 3. Spearman rank-order correlations between species abundance, nested rank-order of sites, and independent variables.

Species	Frequency class	Nested rank-order of sites	Area	Mean elevation	Habitat heterogeneity	Mean density	Isolation
<i>Larrea tridentata</i>	1	-0.34	-0.11	-0.34	-0.06	-0.47*	0.26
<i>Lycium</i> sp.	1	0.03	-0.002	0.28	-0.02	0.15	-0.18
<i>Encelia farinosa</i>	1	0.21	0.05	0.31	0.10	0.34	-0.003
<i>Opuntia acanthocarpa</i>	1	0.56*	0.52*	0.44*	0.30	0.48*	0.07
<i>Ambrosia deltoidea</i>	1	0.44*	0.30	0.53*	0.38	0.53*	0.16
<i>Hyptis emoryi</i>	2	0.49*	0.28	0.50*	0.14	0.15	-0.04
<i>Bebbia juncea</i>	2	0.39	0.25	0.24	0.16	0.27	-0.11
<i>Ephedra fasciculata</i>	2	0.53*	0.39	0.50*	0.36	0.06	0.30
<i>Carnegie gigantea</i>	2	0.63*	0.66*	0.45*	0.52*	0.22	0.36
<i>Eriogonum fasciculatum</i>	2	0.48*	0.34	0.46*	0.29	0.08	-0.10
<i>Fouquieria splendens</i>	2	0.76*	0.75*	0.56*	0.66*	0.18	0.46*
<i>Baccharis sarothroides</i>	3	0.24	0.19	-0.03	0.19	0.12	0.30
<i>Olneya tesota</i>	3	0.36	0.51*	0.06	0.32	-0.39	0.28
<i>Prosopis velutina</i>	3	-0.24	-0.08	-0.34	-0.16	-0.34	0.08

Notes: Abundance is expressed as the mean number of individuals for the species named, sampled from 100-m<sup>2</sup> quadrats, for each of 22 sites. Frequency class designations are: (1) common species (present in at least 19 out of 22 sites), (2) intermediate frequency (present in 8–12 out of 22 sites) and generally following the nested pattern, and (3) intermediate frequency (present in 8–13 sites) in which species presence does not follow the nested pattern.

\*  $P < 0.05$ .

*fasciculata*, *Eriogonum fasciculatum*, and *Fouquieria splendens*) are virtually absent in lower-elevation environments. The other four species occur at lower elevations but are more abundant at higher altitudes. On the other hand, abundances for *Opuntia acanthocarpa*, *Carnegie gigantea*, and *Fouquieria splendens* are more highly correlated with area than mean elevation or habitat heterogeneity, which is suggestive of area effects attributable to either extinction or passive sampling.

Analysis of the relationship between species abundance and nestedness within single habitat types shows that abundance for four focal species declines down the nestedness gradient from species-rich to depauperate sites (Table 4). Given that these data are restricted to a single habitat type, this analysis demonstrates that nestedness at this scale is driven by mechanisms other than habitat heterogeneity, which is an island-level variable. Furthermore, since nested rank-order of sites

for habitats and the area of washes and slopes facing north and east are significantly correlated, this suggests an area effect influencing nestedness at the habitat level. For *Ephedra fasciculata* and *Fouquieria splendens*, elevation is the likely mechanism operating, since these are higher-altitude species; this is true to a lesser extent for *Carnegie gigantea*, which may be observed at lower elevations but is more abundant on the upper slopes.

However, for *Bebbia juncea*, which is primarily found in the wash habitat, this result is strongly suggestive of extinction or passive sampling. Individual washes at lower elevations are necessarily larger than those upslope, since water volume drained per wash increases as smaller tributaries merge. In the Phoenix metropolitan area, washes are more likely than mountain range habitats to experience fragmentation effects, since most mountains are preserved intact to their bases where they transition to the plains. Washes, on the other hand, are

TABLE 4. Spearman rank-order correlations between species abundance and the nested rank-order of sites for habitat types.

Species	Frequency class	North-facing slope	South-facing slope	East-facing slope	West-facing slope	Wash
<i>Larrea tridentata</i>	1				-0.36	
<i>Lycium</i> sp.	1					0.41
<i>Encelia farinosa</i>	1		-0.05			
<i>Opuntia acanthocarpa</i>	1	0.28				
<i>Ambrosia deltoidea</i>	1	0.32				
<i>Hyptis emoryi</i>	2	0.42				
<i>Bebbia juncea</i>	2					0.49*
<i>Ephedra fasciculata</i>	2	0.47*				
<i>Carnegie gigantea</i>	2			0.53*		
<i>Eriogonum fasciculatum</i>	2	0.20				
<i>Fouquieria splendens</i>	2			0.64*		
<i>Baccharis sarothroides</i>	3					-0.10
<i>Olneya tesota</i>	3					0.07
<i>Prosopis velutina</i>	3					-0.30

Note: Habitat types indicated for each species are those in which species achieved maximum abundance in terms of mean density of individuals per quadrat.

\*  $P < 0.05$ .

usually disturbed or transformed into drainage structures outside preserves, eliminating habitat for desert vegetation.

Therefore, connectivity between washes is disrupted with fragmentation. While the plains are also vulnerable to fragmentation effects, vegetation in the flatlands is thinner and more dominated by generalists that reach higher abundances on slopes. *Lycium* sp. falls just short of significance; though *Lycium* sp. prospers best in the wash habitat, it is more of a generalist than *Bebbia juncea*, and may be found in the other habitats.

Analyses of species abundances have demonstrated that species within a community can respond to fragmentation in varied and potentially contradictory ways. In this study, most species were more abundant in the species-rich islands. Two species, *Larrea tridentata* and *Prosopis velutina*, had negative correlations that were short of significance, either due to subtle responses or small sample sizes. However, these species were more abundant in smaller, depauperate sites. This is intuitive, since parcels not catastrophically disturbed are able to support stands of woody desert vegetation; as taxa are extirpated from stressed areas, other resilient species will replace them. *Larrea tridentata* is a widespread and resilient shrub that can withstand stressors many other species cannot (Gardner 1951, Reynolds 1986, Whitford et al. 2001), and can live for hundreds or even over a thousand years provided their substrate soils remain intact (McAuliffe 1994, 1999). *Prosopis velutina* has increased within deserts and rangelands in Arizona, likely resulting from historical cattle grazing and/or fire exclusion (Bahre and Shelton 1993).

As one would expect for an archipelago of remnant patches, there was no evidence for colonization as a mechanism spawning nestedness in woody vegetation. Such a result is not surprising for long-lived woody species fragmented in relatively recent times. This does not necessarily mean that successful migration and recruitment of propagules has not occurred in this system, but that its cumulative effect would be much weaker than other mechanisms contributing to nestedness. Under normal circumstances, the probability of successful recruitment in existing stands of long-lived woody desert species is very low, which further diminishes the expectation of colonization from other islands (Went 1948, Niering et al. 1963, Shreve and Wiggins 1964, Barbour 1968, McAuliffe 1986, Bowers and Turner 2002, Bowers et al. 2004). Fire may remove woody vegetation (Cave and Patten 1984, Schmid and Rogers 1988, McAuliffe 1995), but unless an island is completely consumed, local sources of seed will usually contribute many more seeds than more distant locations. Fortunately, scorched areas are currently less common than areas that have not been burned.

Phenomena that bring about nestedness can have varied effects on species in a community (Patterson 1987, Simberloff and Martin 1991, Kadmon 1995, Wright et al. 1998, Honnay et al. 1999). Even though

species may respond to different mechanisms, cumulative effects can reinforce each other to contribute to an aggregate pattern. This appears to be the case in this study. Some species tend to occupy less common environments found only at upper elevations, so they will only be present in higher mountainous remnants. Other species may be vulnerable to local extinction by directional selection or generalized disturbance. Smaller islands lack buffer zones, so that their limited expanse is exposed to repeated penetration by people from the city. If species are consistent across sites in their extinction vulnerabilities, the nested pattern will emerge (Patterson 1987). It is instructive to conceive of the mechanisms as filters (Wright et al. 1998). Species respond individually to patterns and processes in nature, with the collective outcome of nestedness resulting from multiple contributors.

#### Further questions

There remain several unknown matters regarding nestedness in this system. It is unclear whether a dynamic or static mechanism is the predominant force structuring nestedness. A multitude of mechanisms appear to contribute to the nested pattern, though their relative roles are unknown. Additionally, for these long-lived species, how much of their community structure was determined before or after fragmentation? The extent to which species distributions were directly affected by fragmentation or existed prior to the separation of the sites is uncertain. A potential approach would be to designate and sample control areas similar in dimensions to this system's archipelago in continuous desert terrain to enable comparison (e.g., Harrison 1997). However, it would be difficult to match the distinctive altitudinal and biogeographic site characteristics to allow comparability between the patchy and control areas in this case. A detailed demographic survey, preferably over a lengthy time scale, would be useful for better characterizing the current state and projecting the future status of remnant populations.

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## APPENDIX A

Map of study site locations (*Ecological Archives* E089-138-A1).

## APPENDIX B

Nested rank-order of study sites and values for independent variables (*Ecological Archives* E089-138-A2).