

URBANIZATION AND SPIDER DIVERSITY: INFLUENCES OF HUMAN MODIFICATION OF HABITAT STRUCTURE AND PRODUCTIVITY

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Abstract. As a part of the Central Arizona–Phoenix Long-Term Ecological Research project, we determined how land-use alteration influenced spider and harvestman diversity. We sampled spiders in six habitat types (desert parks, urban desert remnants, industrial, agricultural, xeric- and mesic-residential yards) and tested how habitat type and productivity affected spider diversity and abundance. As expected, agricultural fields and mesic yards were more productive than the other, xeric habitats. These more productive habitats were characterized by higher abundances but lower spider diversity and were dominated by *Lycosidae* (wolf spiders), followed by *Linyphiidae* (sheet-web weavers). The increase in wolf spider abundance was positively correlated with habitat productivity and negatively correlated with the abundance of other predatory arthropods that might compete with, or prey upon, wolf spiders.

Temporal changes in productivity affected spider abundance. After an El-Niño winter (May 1998), spider abundance was five times higher than after an extremely dry winter (May 2000). The differences in spider abundance between agricultural fields and the four xeric habitats were profound in 2000 but moderate in 1998, suggesting an interaction between the effects of natural and anthropogenic factors on spider populations. Compared with xeric habitats, the El-Niño effect was less profound in agricultural sites, suggesting that human land modification mollifies seasonal effects. We suggest that habitat structure and productivity alteration may change community structure, as the urban or agricultural habitats favor one or a few preadapted taxa over many others. Incorporation of large fragments of natural habitats into future landscape planning in urban environments may be important for conservation of rich spider communities.

Key words: arthropod communities; CAP LTER; diversity, spiders; El-Niño; *Lycosidae*; Sonoran desert; urbanization.

INTRODUCTION

Studying ecological patterns and processes in urban environments is a relatively new direction in ecology (Grimm et al. 2000). The lack of ecological studies in urban environments is especially crucial in the field of conservation biology (Miller and Hobbs 2002). During the last two decades, ecologists have made preliminary forays into urban ecology by studying how biological communities and populations change along urban–rural gradients throughout the world. To date, most studies on wildlife in cities have focused on birds (reviewed by Marzluff et al. 2001). We know much less about other vertebrates and almost nothing about the effect of human activities in heavily populated areas upon arthropod communities (McIntyre 2000). Furthermore, the few studies focusing on urbanization and arthropod communities have mainly tested the effect of fragmentation of natural habitats due to urbanization (Miyashita

et al. 1998, Bolger et al. 2000, Gibbs and Stantos 2001, Gibb and Hochuli 2002). These studies focused on the changes in arthropod community composition in forest or scrub fragments, ignoring the arthropod communities that inhabit the urban habitat.

Studying arthropod communities in urban environments is important for several reasons. Habitats are becoming increasingly dominated by human-related factors and processes (Grimm et al. 2000, Miller and Hobbs 2002), yet most ecological studies focus on more natural and less human-altered ecosystems. Furthermore, it is critical to understand if different taxa respond to alterations in landscape structure in the same way. For example, urban bird communities increase in total abundance but decrease in species diversity compared to nonurban communities (Marzluff 2001). As the mechanisms are yet unclear (Marzluff et al. 2001), studying patterns in other taxa may help to generate hypotheses about the processes that shape urban wildlife populations. Another reason for studying arthropods in human-managed environments is that many arthropods are important in agriculture and gardens as pests or biological control agents and in medicine

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(McIntyre 2000). Among the arthropods, spiders are key predators that may also reflect changes in trophic structure in human-altered ecosystems.

Part of the Central Arizona–Phoenix Long-Term Ecological Research (CAP LTER) project is an on-going (since spring 1998) study on ground-dwelling arthropods. The goals of this study are to assess how arthropod communities change in space (between different urban and natural land-use types, or habitats) and time (different seasons and years). McIntyre et al. (2001) summarized the results from the first year of monitoring. Taxonomic richness and abundance were higher in agricultural fields and relatively low in desert sites. Functional groups showed differences in abundance between habitats. Predators and herbivores were most abundant in agricultural sites, whereas omnivores were equally abundant among sites (McIntyre et al. 2001).

In this study, we focus on the predator guild, specifically spiders (order Araneae) and daddy long legs (or harvestmen, order Opiliones). Spiders are abundant and dominant components of the arthropod predatory guild in most communities (Wise 1993), and may be highly influenced by habitat patchiness in general (Whitehouse et al. 2002) and anthropogenic changes in the ecosystem such as urbanization and habitat fragmentation in particular (Miyashita et al. 1998, Bolger et al. 2000). We ask whether spider abundance and diversity are influenced by habitat type within the urban ecosystem and whether differences in habitat productivity affect the spider community.

Productivity is a major environmental axis known to affect species diversity in general (Rosenzweig 1992). Although very productive habitats can support high population densities, for various possible reasons (reviewed by Rosenzweig and Abramsky 1993) their species diversity is often lower than moderately productive environments. The higher productivity in urban environments may be a major factor affecting biological populations (Emlen 1974, Marzluff 2001). Despite these claims, the productivity component and its effect on biological diversity in urban environments have been ignored. Here we test how changes in productivity in both time and space influence spider diversity and abundance. We examine possible bottom-up or top-down mechanisms underlying the observed patterns and suggest future directions for urban landscape planning strategies in terms of conservation of spider diversity.

We used six major habitat types in the greater Phoenix area and sampled spiders each month for three years: desert, urban desert remnants, industrial, agricultural, xeric urban yards, and mesic urban yards. To generate predictions, we placed each habitat on a state space of two major environmental axes: patch size (the result of desert fragmentation) and productivity (the result of desert habitat alteration into residential or agricultural habitats that receive supplemental water).

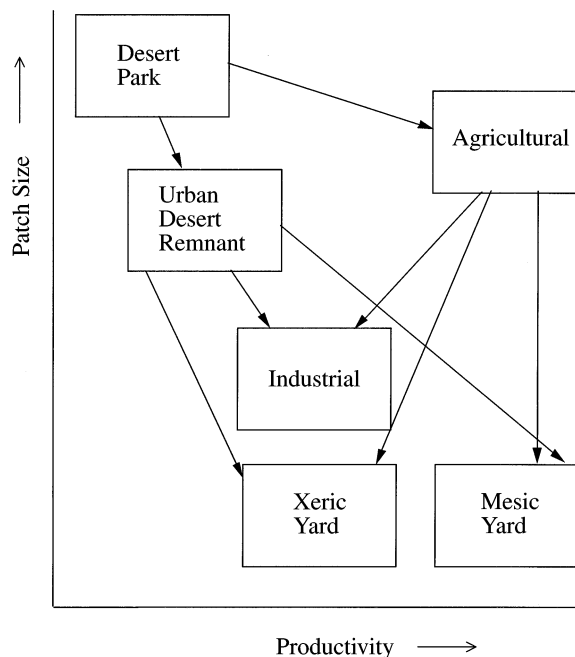


FIG. 1. Schematic showing the estimated location of the six studied habitats along productivity and spatial scale (patch size) axes. Arrows represent development processes in which habitat size, structure, and productivity are being modified.

The estimated location of each habitat on the state space and the relationships between the habitats are given in Fig. 1. Based on these criteria we made two predictions:

1) Spider diversity should peak in urban desert remnants and industrial sites. Diversity will be lower in: (a) undisturbed desert due to lower productivity, (b) xeric yards due to a decrease in patch size (fragmentation), and (c) mesic yards and agricultural sites due to an increase in productivity.

2) Spider abundances should be greater due to high productivity (a) in mesic yards and agricultural sites in comparison to the other four habitats and (b) during a wet El-Niño year (1998) compared with an unusually dry year (2000).

METHODS

Study area

The ground arthropod population project of the CAP LTER has been designed to sample the major land-use types (habitats) in the greater Phoenix area. In the first year, arthropods were sampled in 16 sites classified into four habitats. McIntyre et al. (2001) defined and described in detail the criteria for habitat classification of these habitats. The sites covered a wide geographic range around Phoenix and represented the most abundant forms of land use in the area (McIntyre et al. 2001). The habitats were:

1) Urban desert remnants: characterized by Sonoran desert vegetation and lacking any built structures, these

sites represent an early stage of desert fragmentation by urbanization.

2) Agricultural fields: mostly alfalfa fields, representing alteration of the extremely dry desert land into extremely productive and moist habitat.

3) Industrial sites: nonresidential commercial structures or warehouses surrounded by yards with Sonoran desert vegetation subjected to no or very little irrigation.

4) Xeric residential yards: A single-family house surrounded by xeriscaped yard (nonturf, gravel, and a high proportion of Sonoran desert vegetation subjected to irrigation).

Though industrial sites and xeric yards may undergo changes in habitat structure, they are in most cases characterized by desert vegetation, and therefore can be treated as representing mainly a progressed stage of desert fragmentation. The differences between the industrial sites and xeric yards are usually in fragment size (xeric yards are smaller), isolation (due to fencing in xeric yards), and productivity, due to different irrigation regimes.

During the second year of study, eight sites and two additional habitats were included. Since spring 1999, arthropods were sampled in 24 sites (four replicates of each of the six habitats). During the study period, two sites had to be relocated due to development, bringing the total number of sites to 26:

5) Desert parks, included two new sites and two old sites. Though increasingly surrounded by suburbs, desert parks are still connected to the continuous Sonoran desert around the Phoenix metropolis. Accordingly, two new urban desert remnant sites were added to class 1.

6) Mesic yards, representing a different kind of a moist productive habitat than agriculture. Mesic yards are characterized by lawns (>50% of the total yard), high proportion of exotic plants, and irrigation systems.

The six habitats can be classified along a patch size/productivity gradient (Fig. 1). Understanding the processes that lead to the creation of each habitat along the axes of habitat fragmentation and productivity is important in order to understand how these processes may affect spider communities in an urban ecosystem.

Assessing the degree of fragmentation

We assessed the degree of landscape fragmentation by calculating the area of contiguous patch type (representing habitat) adjacent to, and including, each arthropod sampling location. A 1998 land cover classification of the Phoenix metropolitan area derived from Landsat Thematic Mapper (TM) data (Stefanov et al. 2001) was used as the base data set for the calculation of contiguous patch area. This land cover classification has the spatial resolution of TM data (28.5×28.5 m/pixel). The 12 original land cover classes of the 1998 classification were recoded into six patch types (desert, urban desert remnants, industrial, agricultural, xeric yard, and mesic yard) to ensure comparability with the

existing patch classification scheme. The resulting raster data set was converted into a vector shapefile format in order to group similar patch type pixels together as single polygons using an edge-to-edge rule (i.e., diagonally adjacent pixels are not included in the total area calculation).

Arthropod sampling

We collected spiders and harvestmen (orders Araneae and Opilionida) with other arthropods using 10 dry unbaited pitfall traps at each of the 26 sites. Traps were spaced 5 m apart along a line transect (straight line, unless constrained by property boundaries at residential sites). Traps consisted of a 500-mL plastic cup stacked inside another cup, with the lip of the inner cup set flush to the ground surface. Traps were set for 72 consecutive hours each month. The inner cups of each trap and their contents were then removed without displacing the entire trap. When not in use, traps were tightly closed with plastic lids. Trap contents were collected and preserved in 70% ethanol, and spiders were identified to a family. Voucher specimens are housed in the Department of Biology at Arizona State University, Tempe.

Pitfall traps may have disadvantages when trying to assess species diversity, because they do not sample the entire community (Adis 1979, Topping and Sunderland 1992). The capture rate of spiders in pitfall traps is a function of both the activity level of the spider and its ability to escape from pitfall traps. In addition, *Linyphiidae* and *Lycosidae* species are often overrepresented in pitfall traps with respect to actual field density (Topping and Sunderland 1992). Nevertheless, pitfall traps allow a comparison of the relative abundance of different families between different sites and are therefore useful tools for indicating differences between communities at different sites. As pitfall traps are more easily standardized than some other sampling techniques they are especially useful in long-term studies, such as this one.

Climatic and remote sensing measures

Remotely sensed data were used to characterize vegetative biomass and ground temperature conditions at the pitfall trap sites during two different climatic regimes. To compare the climatic conditions between an El-Niño year (1997/1998) and an extremely dry year (1999/2000), we calculated the average monthly rainfall for the eight months before satellite multispectral data were acquired (October–May for each year). These data for the Phoenix area were available from the departments of Geography and Geological Sciences at Arizona State University. Landsat Thematic Mapper (TM) data were acquired on 24 May 1998 and Enhanced Thematic Mapper Plus (ETM+) data were acquired on 21 May 2000. The ETM+ is the successor instrument to the TM. It has similar band arrangements and wavelength coverage that allows direct comparison

of data from both sensors at a ground resolution of 30 m/pixel (Parkinson and Greenstone 2000).

To quantify productivity in a given pixel, we calculated a normalized difference vegetation index (NDVI) for both the TM and ETM+ data sets. The NDVI calculates the relative percentage of actively photosynthesizing vegetation per pixel by rationing reflectance values in the visible red (low for plants) and near-infrared (high for plants) wavelengths (Botkin et al. 1984). The resulting values represent a spatial map of actively photosynthesizing vegetation and its abundance. Deserts typically have low NDVI values corresponding to low vegetation abundances and lack of leafy species, while forests have high values corresponding to high densities of leafy species (Turner et al. 2001). The NDVI values were calculated using atmospherically corrected reflectance data using the MODTRAN radioactive transfer code incorporated into the ATCOR software package (Richter 1999).

Differences in spider abundance between habitats may also be influenced by microclimatic conditions. Therefore, we calculated surface brightness temperatures (SBT) for the sample sites using the atmospherically corrected TM and ETM+ data. The SBT is the result of both radiant heating by the sun and stored energy released by emittance from surficial materials (Jensen 2000). As such, SBT provides a reasonable measure of the sensible heat a ground-dwelling organism would experience. The thermal band from each sensor (10.4–12.5 μm) was coregistered and resampled down to 30 m/pixel ground resolution to allow for comparison between the two data sets and vegetation index data. An average SBT was obtained from a 3×3 pixel region surrounding each sample site to minimize potential colocation error between the ground survey points and satellite pixels.

Statistical analysis

To describe gradients in spider distribution we applied canonical correspondence analysis (CCA) using CANOCO (ter Braak 1986). The data set included the total abundance of each spider family in each of the 26 sites. Environmental data included the six habitat types as dummy variables.

Due to logistical problems, several sites were not visited continuously on a monthly basis throughout the three years of study. Therefore, we pooled all time periods and calculated average spider abundance as the number of spiders per sample per site. We used ANOVA to assess the differences in diversity and abundance between sites and linear regression models to assess how site productivity and presence of nonspider predator affect spider abundance and diversity.

The differences in sampling effort among the 26 different sites could bias the number of spider families sampled (the random sample hypothesis sensu Connor and McCoy 1979). Rosenzweig (1995) suggested using diversity indices to control for sample size. Since dif-

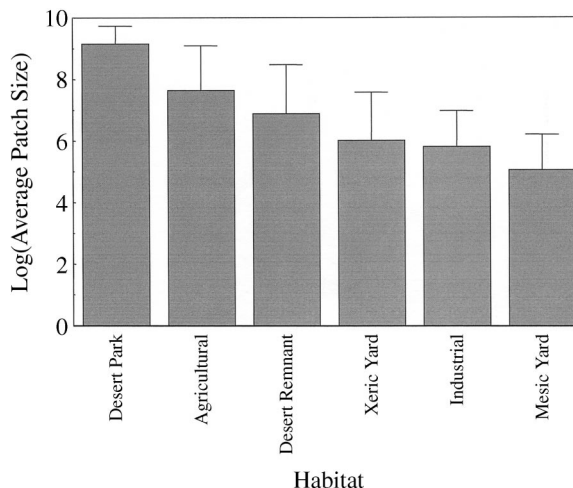


FIG. 2. Differences in patch size (in square millimeters) between six habitat types in the Phoenix area. Error bars represent +1 SD.

ferent diversity indices have both advantages and disadvantages (Rosenzweig 1995) and may yield different results, we used three indices to control for sampling artifacts: (1) Simpson index (Simpson 1949) is particularly efficient in detecting dominance but may be affected by sample size, (2) Fisher's alpha (Fisher et al. 1943) does not detect dominance but is unbiased by sample size, and (3) rarefaction (Sanders 1968), a method that reduces all samples to the same level and yields comparable species accumulation curves. The analytic rarefaction program we used was developed by S.M. Holland and is available on the web.⁶

RESULTS

Habitat patch size

The habitat differences in patch size are shown in Fig. 2. Examination of the area means for the six habitat types suggests a progression of fragmentation similar to that presented in Fig. 1 with one exception. Industrial sites were smaller patches than xeric yards. Total mean contiguous area decreases in the progression desert > agricultural > desert urban remnants > xeric yards > industrial > mesic yard. There is a large range of area values within these classes; this reflects the highly heterogeneous spatial patch structure of the Phoenix metropolitan region. Nevertheless, a general trend of fragmentation of spider habitat can be discerned using the mean patch area values.

Spider abundance and distribution

A total of 5574 spiders from 24 families were trapped between April 1998 and March 2001 in the 26 study sites (Appendix). In the two most mesic habitats 76.19% of the spiders were trapped: 3187 (57.09%) in

⁶ URL: www.uga.edu/~strata/software/AnRareReadme.html

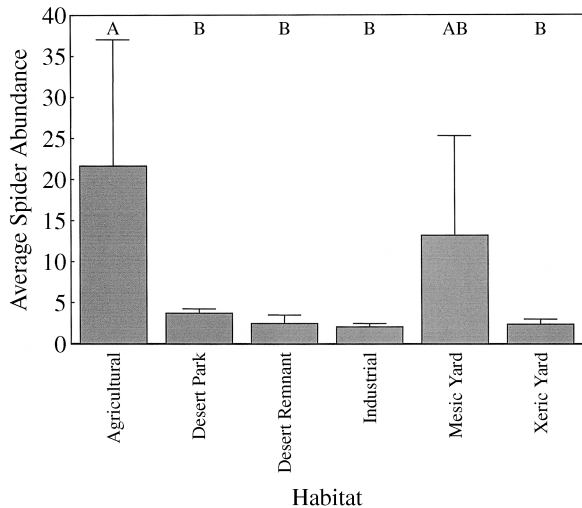


FIG. 3. Differences in spider abundance (spiders per sample) between six habitat types in the Phoenix area. Different letters above bars indicate significant differences ($P < 0.05$). Error bars represent $+1$ SD.

agricultural sites, and 1066 (19.10%) in mesic yards. Spider abundance was also the highest in these habitats, with 21.62 individuals per site per month found in agricultural fields and 13.67 individuals found in mesic yards. The most abundant family was *Lycosidae* (wolf spiders) with 3280 individuals, representing 58.8% of the total, followed by *Linyphiidae* with 596 individuals

(10.7% of the total). These two families were more abundant in agricultural fields and mesic yards than in the other four xeric habitats. Lycosids increased from 10–20% of the spider assemblages in the xeric habitats to 70–80% in agricultural fields and mesic yards. Linyphiids increased from 3–8% to 12–14% in the same habitats. The highest number of spider families (19) was found in desert remnants and the lowest (14) in xeric yards. Total spider abundance differed between habitats (ANOVA, $F = 4.387$, $df = 5,25$, $P = 0.007$). Abundance was the highest in agricultural fields, followed by mesic yards (Fig. 3).

The first axis of the CCA (Fig. 4) accounted for 26% of the spider family variance and separated desert parks and desert remnants from the other, human-managed habitats. This analysis suggests that spiders respond to land-use modification and changes in productivity. The second axis, accounting for 13% of the variance, separated agricultural, mesic yards, and desert sites from desert remnants, xeric yards, and industrial sites. Consequently, the spider community in xeric yards was similar to industrial sites, whereas the two most productive habitats, agricultural and mesic yards, had the most similar spider assemblages. The species–environment correlations were 0.88 on the first axis and 0.90 on the second axis. A Monte-Carlo simulation with 499 permutations indicated that species distribution along the axes was not random (first canonical axis, F ratio = 4.546, P value = 0.002; all canonical axes, F ratio = 2.310, P value = 0.002).

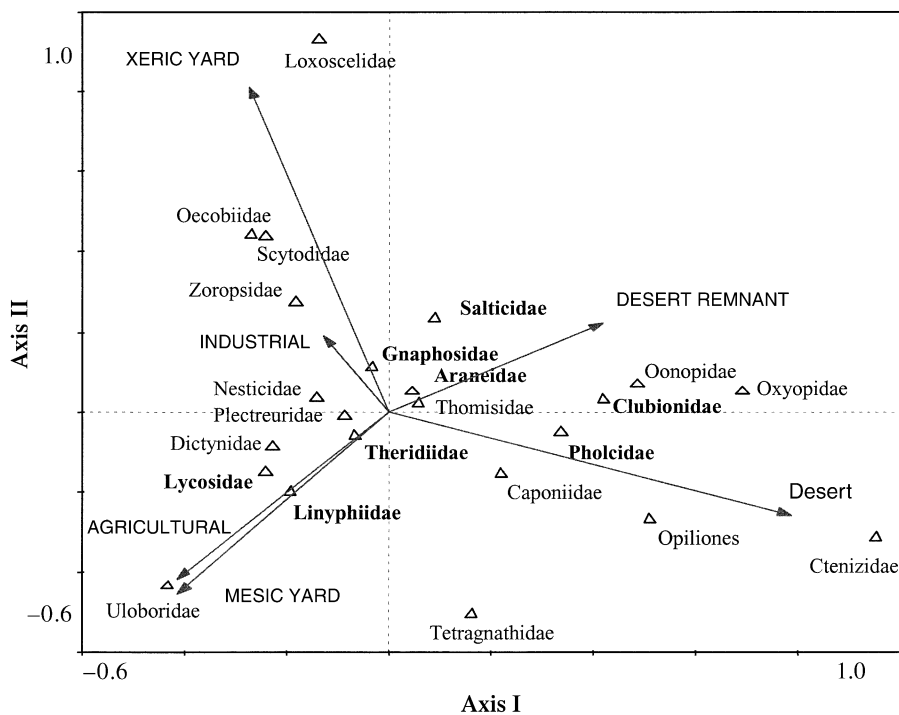


FIG. 4. Ordination diagram of the first two axes of canonical correspondence analysis for 23 spider families and six habitat types used as dummy variables. Arrows represent directions of greatest change in environmental variables. The eight most common families, making up 94.4% of all spiders collected, are boldface.

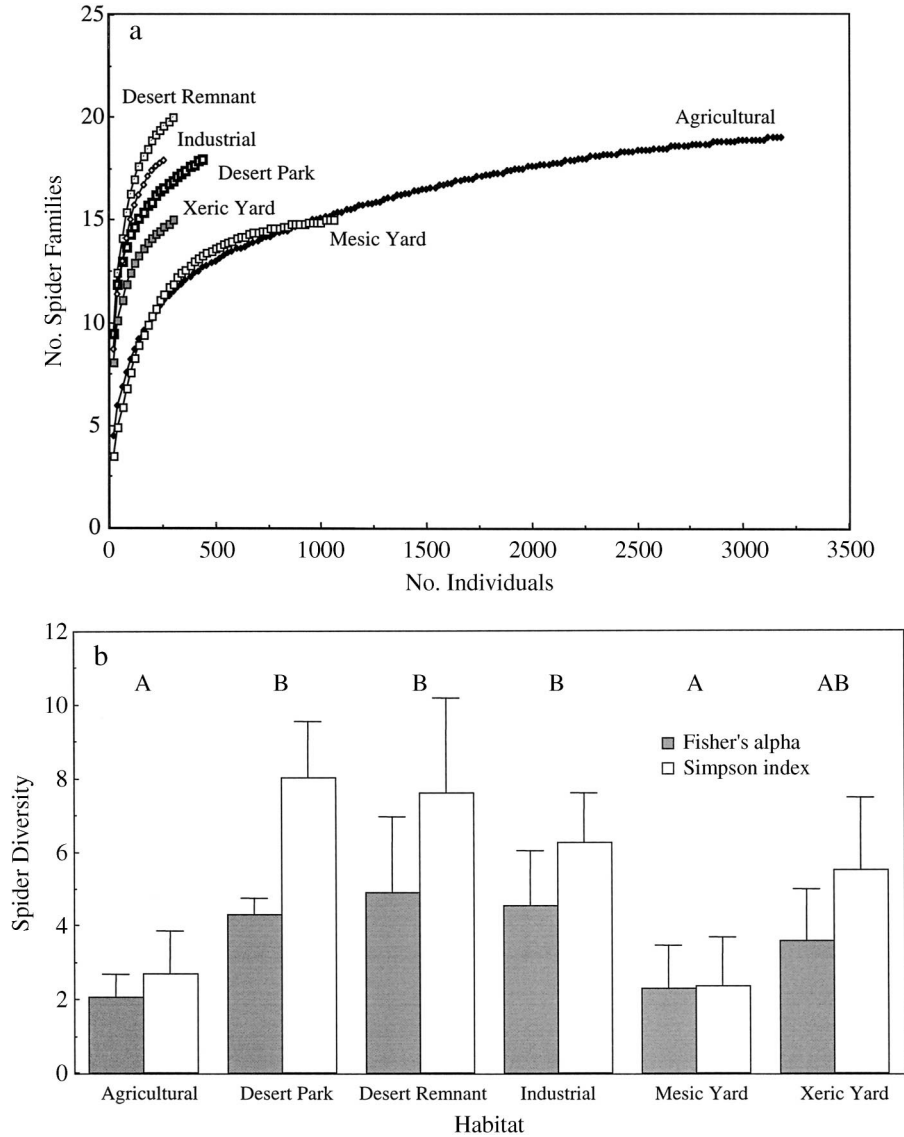


FIG. 5. Differences in spider diversity among six habitat types in the Phoenix area. (a) Rarefaction curves showing the expected number of spider families for any given number of individuals. (b) Average Simpson index and Fisher's alpha values. Different letters above bars indicate significant differences. Error bars represent +1 SD.

The eight most common families, making up 94.4% of all spiders collected, are marked bold in Fig. 1. The most common families are located around the origin (indicating that they were equally common in all habitats) or more associated with the mesic and agricultural sites, which were the most productive sites and where spider abundance was high. *Lycosidae*, which makes up >58% of the total abundance of the total trap, was one of the families most strongly associated with mesic and agricultural habitats, although they were also found in other habitats. The large tail of families that extends along the desert parks and remnants axis indicates that less common families were found at these sites. The tail also includes two commonly found families, Clu-bionidae and Pholcidae, indicating that these two fam-

ilies are strongly associated with desert parks and remnants.

Diversity

We used three indices to calculate diversity. All indices indicated that diversity was the lowest where spider abundance was the highest (i.e., in agricultural fields and mesic yards). These were Fisher's alpha (ANOVA, $F = 3.64$, $df = 5,25$, $P = 0.017$), Simpson index (ANOVA, $F = 10.139$, $df = 5,25$, $P < 0.001$), and rarefaction curves (Fig. 5). Simpson index and Fisher's alpha were highly correlated across all sites (Pearson correlation, $r^2 = 0.71$, $P < 0.001$). Urban desert remnants showed the highest diversity according to both Fisher's alpha and rarefaction. Simpson index indicated

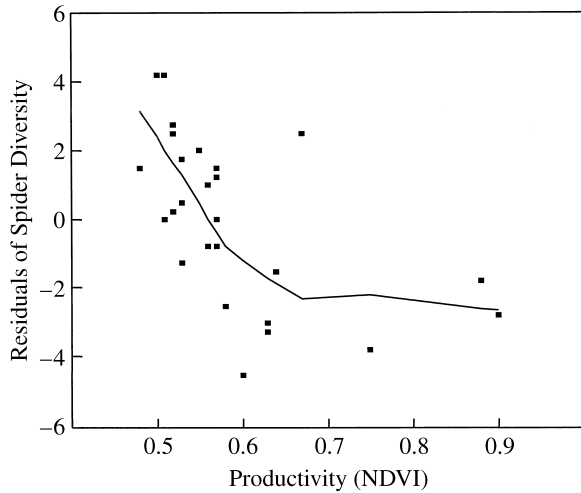


FIG. 6. The relationship between spider diversity and habitat productivity in the 26 study sites. NDVI refers to the normalized difference vegetation index.

a slightly lower diversity in this habitat than in desert parks, suggesting that spider assemblages in desert parks are more evenly distributed than in desert remnants (Fig. 5b). Diversity in xeric yards and industrial sites was moderate, but closer to desert remnants and desert parks than to agricultural sites and mesic yards.

Simpson index and rarefaction indicated that the lowest species diversity was in mesic yards. Though the rarefaction curve for this habitat appears similar to the agricultural habitat, it levels off earlier (Fig. 5a), whereas the agricultural habitat curve continues to increase moderately (Fig. 5b). Low Simpson index values in these two habitats (Fig. 5a) indicate highly dominant spider assemblages caused by the increase in the proportion of Lycosidae.

Spider diversity and habitat productivity

To test how habitat productivity influences spider diversity we used a multiple regression model in which habitat was a dummy variable. Of the six independent variables, (NDVI plus five dummy variables) only NDVI was significant ($r^2 = 0.63$, $P < 0.001$ for NDVI, $F = 5.32$, $P = 0.002$ for the whole model). We then reran the analysis with the dummy variables only, extracted the residuals of spider diversity, and plotted them against NDVI as a sole independent variable. The results are shown in Fig. 6. To fit the nonlinear relationship between diversity and productivity we applied a locally weighted regression scatter plot smoothing (lowess; Neter et al. 1996).

The results indicate a decrease in spider diversity with habitat productivity. The NDVI data are taken from May 2000, an extremely dry year with a good contrast between desert and human-managed sites. The apparent decrease in spider diversity when NDVI was measured following an El-Niño year (May 1998) was not significant. Replacing family richness with diver-

sity yielded similar results suggesting that the decrease in diversity was not due to a sampling artifact. The overall low fit is due to the high variance in richness/diversity between sites of low productivity. The few very productive sites (mostly agricultural and mesic yards) had lower diversity than most desert/xeric sites.

El-Niño effects on spider abundance

Compared with winter 1999/2000, the monthly average precipitation during winter 1997/1998 (October 1997–May 1998) was higher (Fig. 7a). Consequently, NDVI values measured in May 1998 were higher than those measured in May 2000 (Fig. 7b). The differences were not significant (paired t test, $t = 1.78$, $df = 25$, $P = 0.087$), probably because a few agricultural and mesic yard sites had higher values in 2000. Removing the mesic sites (where spiders were not sampled in

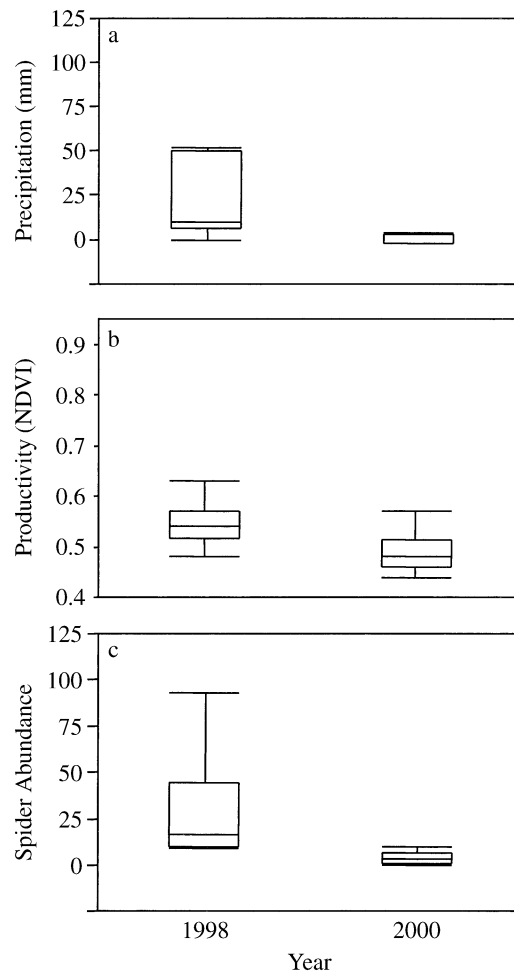


FIG. 7. Differences in (a) precipitation, (b) productivity (NDVI), and (c) spider abundance between May 1998 (following an El-Niño year) and May 2000 (following an extremely dry year). NDVI values and spider abundance are averaged across all but mesic habitats (where spiders were not sampled during the first year of study).

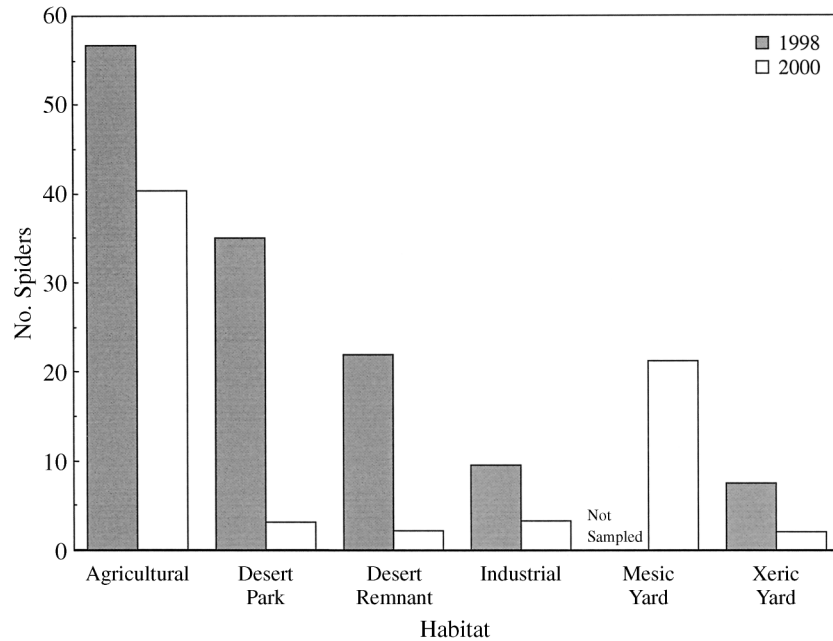


FIG. 8. Comparison of spider abundance between May 1998 and May 2000 within each habitat.

1998) from the analysis yielded significant differences (paired t test, $t = 3.440$, $df = 20$, $P = 0.003$).

To test whether the El-Niño event affected spider abundance, we compared spider abundance between May 1998 and May 2000. Average spider abundance (in all 14 sites where it was measured in both years) was five times higher in 1998 than that in 2000 (paired t test [log number of spiders], $t = 8.27$, $df = 13$, $P < 0.001$, Fig. 7c). We further tested whether this El-Niño effect occurred at the local (site) scale by regressing the “delta spider abundance” (the within-habitat differences in spider abundance) between years against the delta NDVI values, but found no correlation (linear regression, $r^2 = 0.023$, $P = 0.60$).

Spider abundance was lower in the drier spring (2000) in all five habitats (mesic yards were not sampled in 1998) than in the El-Niño spring of 1998 (Fig. 8). Abundance also decreased in the agricultural habitat (where it was the highest in both years), although irrigation is likely to compensate for the decrease in precipitation. However, whereas in May 2000 spider abundance in the agricultural habitat decreased to 71% of the abundance in May 1998, it decreased to 9% in desert parks, 10% in desert remnants, 35% in industrial, and 28% in xeric yards. In 1998, spider abundance in these habitats ranged between 13% and 62% of the abundance in the agricultural habitat. In 2000 it ranged between 5% and 8% of the abundance in agricultural fields.

In general, the trends in surface brightness temperature (SBT) variation were similar between 1998 and 2000, with the 2000 temperatures being consistently higher than 1998 (linear regression, $SBT_{2000} = 12.57$

+ 0.85 × SBT_{1998} , $r^2 = 0.65$, $P < 0.001$). This is in agreement with recorded precipitation and NDVI data; in both years SBT decreased with increasing NDVI, but this decrease was not significant in 1998, probably due to high vegetation density at most of the 26 sites. In contrast, the lower 2000 NDVI values at sites that are not actively managed and hence more susceptible to variations in climate were probably the cause of the sharp decrease in SBT with NDVI (linear regression, $SBT = 66.97 - 34.85 \times NDVI$, $r^2 = 0.83$, $P < 0.001$).

Total spider abundance was negatively correlated with SBT in both years (Fig. 9). We also found a negative correlation between SBT and spider abundance measured in the same months (May 1998 and May 2000), but this correlation was significant only in 2000 (spider abundance = $95.30 - 1.82 \times SBT$, $r^2 = 0.71$, $P < 0.001$).

Population level: bottom-up/top-down effects

We further tested for possible effects of prey abundance, predators, and habitat productivity on spider abundance. Here, we focused on the wolf spiders (*Lycosidae*). This family appears to be a key group, given its high abundance, especially in mesic yards and agricultural fields. We used a stepwise multiple regression model in which the dependent variable was wolf spider abundance, and the three independent variables were productivity (NDVI), prey abundance (Collembola, Diptera, and aphids, following Toft 1999), and competitor/predator abundance. This latter group included mantises (Order Mantodea), ant lions (Neuroptera), scorpions (Scorpiones), pseudo-scorpions (Pseudoscorpiones), and solpugids (Solifugae). These data were

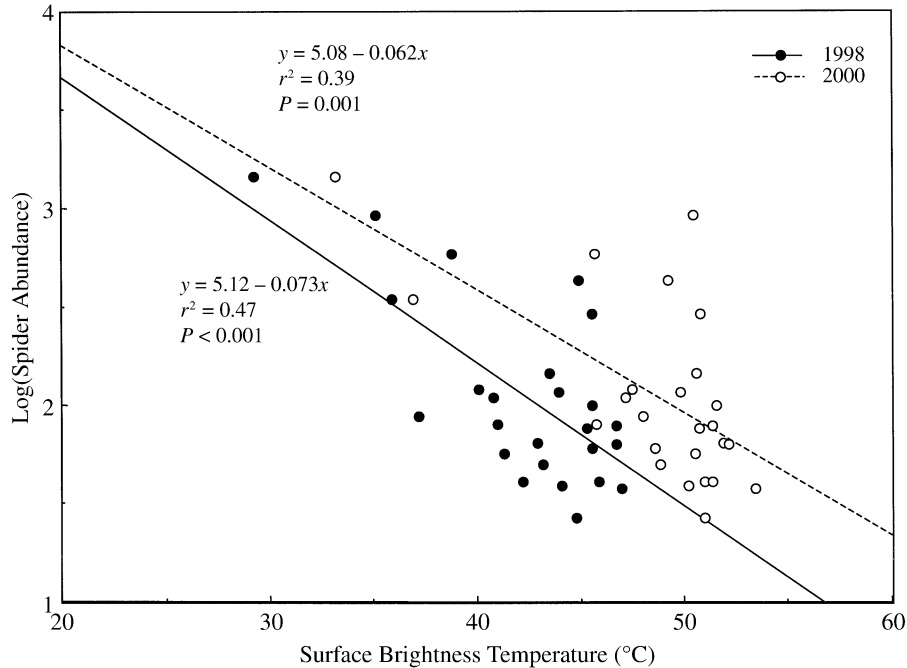


FIG. 9. The relationship between spider abundance and surface brightness temperature in the 26 study sites.

taken from the CAP LTER data set, collected simultaneously at the same sites. Individually, all three independent variables significantly correlated with wolf spider abundance. Wolf spider abundance increased with productivity and prey abundance and decreased with other predator arthropod abundance. NDVI was the first variable to enter the regression equation followed by other predator arthropod abundance (Table 1). Prey abundance did not account for more variance and was removed from the model. Accounting for 35.8% of the total variance in wolf spider abundance (Table 1), the model's equation was:

$$\begin{aligned} \log(\text{wolf spider}) &= 0.014 + 3.089(\text{NDVI}) \\ &\quad - 0.478 \log(\text{other predator arthropod}). \end{aligned}$$

DISCUSSION

Anthropogenic effects, habitat management, and conservation of spiders have been thoroughly studied in agricultural ecosystems (reviewed by Bell et al. 2001). Much less is known about how urbanization influences spider communities. Land-use alteration by humans changes habitat structure and increases habitat fragmentation and site productivity (Gober et al. 1998, Lopez et al. 2002). The major response of spiders appears to be a general decrease in diversity (Fig. 5) and an increase in total abundance (Fig. 3). These processes are similar to the general pattern described for urban birds (Marzluff 2001). The increase in spider abundance is mostly due to a sharp increase in wolf spider (*Lycosidae*) abundance, and accordingly in their dom-

inance. Wolf spiders thrive in mesic yards and agricultural fields. The dramatic increase in their proportion in these sites radically changes community composition and local diversity. Furthermore, the second most abundant family, *Linyphiidae*, is about twice as common in agricultural fields and mesic yards compared with the other four xeric habitats. Interestingly, these two families account for most species and individuals found in agricultural fields throughout central and northern Europe (Toft 1999). Furthermore, the similarities in community composition between the American southwest and Europe agree with the idea suggested by Blair (2001) that urbanization brings about the creation of homogeneous bird fauna. Our results suggest that this homogenization may also include other taxa and other human-managed habitats such as agricultural fields.

The high dominance of wolf spiders in productive habitats decreases spider diversity (Fig. 5). However, omitting this family from the analysis does not fully compensate for the decrease in diversity, and it remains the lowest in agricultural fields and mesic yards (data not shown). This suggests that increasing habitat productivity causes a general loss in diversity. Families that are adversely affected by desert land development are *Clubionidae*, *Oonopidae*, and *Oxyopidae*. Although uncommon in xeric habitats, these families are absent from highly productive habitats (Fig. 4; Appendix), suggesting that rarer families or species are most susceptible to losses when productivity increases.

The role of habitat productivity

Reviewing results of various studies on different taxa and provinces, Rosenzweig (1992) and Rosenzweig

TABLE 1. The effect of three environmental factors on the abundance of wolf spiders (*Lycosidae*).

A) Regression					
Variable	Coefficient	<i>F</i>	<i>P</i> value	Accumulative <i>R</i> ²	
Constant	0.014	0.019	0.985		
NDVI	3.089	2.485	0.021	0.237	
Other predator arthropod	-0.478	-2.084	0.048	0.358	
Prey (removed)	0.136	0.418	0.525		
B) Anova					
Source	ss	df	Mean square	<i>F</i> ratio	<i>P</i>
Regression	6.654	2	3.323	6.422	0.006
Residual	11.900	23	0.517		

Notes: Stepwise multiple regression model included habitat productivity (normalized difference vegetation index [NDVI] values), prey abundance, and other predator arthropod abundance.

and Abramsky (1993), showed how biological diversity first increases, then decreases with environmental productivity. The diversity-productivity humped-shaped relationship is generally detected across very large spatial scales (e.g., species richness from the tropics to the temperate zone). However, urbanization can be viewed as a process that alters both habitat structure and productivity on local spatial scales.

Controlling for habitat type, our analysis indicates that the increase in productivity was the major cause for the reduction in spider diversity. The relationship between spider diversity and habitat productivity was not unimodal. Spider diversity decreased with productivity with a sharper rate in low productivity sites (Fig. 6). Possibly, the Sonoran desert already represents moderate productivity, and one should sample spiders in more arid deserts, such as the Mojave, for the increasing part of the curve. Our results differ from other studies on the response of arthropod diversity to productivity. Siemann (1998) found an increase in total arthropod diversity, as well as in the predator trophic level, in sites where productivity was experimentally enhanced. Kaspari et al. (2000) found an increase in ant diversity with productivity from deserts to rainforests. The mechanism responsible for the loss of spider diversity in highly productive sites in Phoenix is unclear. Several mechanisms may lead to the same pattern, but even under the same mechanism the results depend on which part of the productivity scale is being measured (Rosenzweig and Abramsky 1993). Siemann (1998) demonstrated how even by using an experimental approach it may be difficult to understand the complex relationship between diversity and productivity. For example, fertilization not only increases productivity, but also plant species diversity. Therefore, it can affect diversity both directly and indirectly. However, the decrease we found in spider diversity may suggest that some of the human-managed habitats are located extremely high on the productivity axis, and lead to low species diversity as predicted by Rosenzweig and Abramsky (1993).

The spider communities in industrial and xeric yards are located somewhere in the middle between desert and mesic sites (mesic yards and agricultural sites) (Fig. 4). As xeric yards contained mainly desert plants, we would have expected their communities to more closely resemble desert communities. However, owners of xeric yards in the Phoenix metropolitan area tend to water these habitats to produce rapid and sustained growth of plants (Martin and McDowell 1999). Thus, supplemental watering increases the productivity of the xeric habitat and spider and prey species may have responded accordingly.

Food abundance and competition

It is not clear how food abundance should affect spider abundance or distribution. Greenstone (1984) showed that spider diversity responded to vegetation structure more than to food abundance, though Bell et al. (2001) argued that changes in food availability affect prey abundance and that shortage of prey may influence growth rate and clutch size. In our study, productivity was the major factor accounting for wolf spider abundance (Table 1). Habitat productivity may confound other variables such as habitat structure or prey abundance—a variable that did enter the multivariate model of wolf spider abundance (Table 1). Competition or predation by other arthropods is not likely to affect wolf spider abundance. Although scorpions, solpugids, ant lions, and mantises were negatively associated with wolf spiders, their abundance accounted for only a minor portion of the variation in wolf spider abundance (Table 1). Vertebrate predators may have an even greater effect on wolf spiders. Foelix (1982) argued against the general overestimation of bird effect on spiders. However, the Phoenix area is very rich in lizards, which appear to be more common in natural, xeric habitats than in agricultural fields.

Since productivity increases in mesic yards and crop fields, the increase in wolf spider abundance may not necessarily involve out-competing other spiders. Indeed, in relatively productive sites local spider com-

munities may be resilient to invasive spider species (Burger et al. 2001). In our study one widespread family, Araneidae, appears in agricultural fields at the same abundance as in other habitats. This family occupies a completely different niche to Lycosidae and therefore is unlikely to be in direct competition. Spider families that vanish or decrease in abundance in agricultural fields or mesic yards may be influenced by high disturbance rates. Mesic yards (mostly lawns) are often subjected to mowing, and agricultural fields are plowed, harvested, and subjected to a high turnover of crop types. Possibly, such disturbed habitats favor Lycosid and Linyphiid species. Lycosids are ground dwellers, and Linyphiidae are "wind dispersed" spiders that build small sheet webs close to the ground. A disturbed habitat where vegetation is close to the ground or removed (such as in a plowed field) may be highly suitable for them. This idea is strongly supported by Nentwig (1988) who found that Linyphiids predominated as pioneer species in intensively cut grass fields but become less abundant as dominance shifted from Linyphiids to Lycosids.

Climatic effects

The higher spider abundance in an El-Niño year (Fig. 7) suggests that extreme differences in annual rainfall between years may dramatically affect spider abundance. It is not clear how general this phenomenon is. McIntyre et al. (2001) found that both abundance and richness of the entire arthropod community correlated with air temperature, but not with rainfall. In contrast, Bolger et al. (2000) suggested that changes in rainfall in southern California might cause seasonal changes in arthropod diversity and abundance.

The lack of correlation between NDVI and spider abundance at the site scale suggest that spider population response to rainfall and changes in vegetation cover may not be obvious across small spatial or temporal scales. NDVI values represent snapshots of the result of a fairly long-term event (months) that affect an area much larger than the sampling points. The patterns described here suggest that spider abundance may show different responses to various biotic, abiotic, and anthropogenic factors, and across different scales of space and time. The decrease in spider abundance in sites where SBT is high is particularly interesting. De Keer et al. (1989) showed how changes in microclimatic conditions due to grassland management influence spider activity. Our results suggest that in addition to such behavioral changes, extreme alteration of microclimatic conditions can also affect spider abundance. The decrease in abundance with SBT may explain the high abundance in mesic yards and agricultural fields (Fig. 9). In addition to the correlation between higher SBT and lower productivity, it is possible that higher SBT directly affects spider diversity and abundance by decreasing the "comfort zone" for pred-

ators, leading to increased migration from areas of high SBT.

The response of spider abundance to the increase in productivity is also not straightforward. Obviously, El-Niño years increase local productivity throughout the environment, especially in desert sites. In May 1998 (El-Niño year), spider abundance was higher than in May 2000 (a particularly dry year) in all habitats (Fig. 7). Interestingly, it was higher by ~50% even in the agricultural habitat. This may reflect the much higher total spider abundance in the environment and the presence of many "floater" spiders in agricultural fields. It may also explain why there is no correlation between NDVI values and spider abundance across all sites. After hatching in spring, and especially in high densities as in El-Niño years, spiders may move across different habitats searching for good quality patches to establish and build webs. During such periods the relationship between spider abundance and habitat structure or quality may not be at equilibrium. Yet, one important pattern that emerges (Fig. 8) suggests that in El-Niño years, the productivity of natural habitats, even deserts, increases to a level similar to that of human-managed habitats. Therefore, a possible effect of agricultural development and urbanization is the cancellation of seasonality.

Management and conservation

The results indicate that a moderate fragmentation of Sonoran desert into urban desert remnants where fairly large desert fragments may exist does not reduce spider diversity. Spider diversity in desert remnants may even exceed diversity in desert parks. However, further desert fragmentation into xeric urban yards decreases diversity. The reasons for this decrease are not totally clear, and correlative studies may not be sufficient for revealing mechanisms. Miyashita et al. (1998), Bolger et al. (2000), and Gibb and Hochuli (2002) all suggested complex mechanisms for the effect of habitat fragmentation on spider abundance. For example, as spiders represent a high trophic level, changes in food abundance due to fragmentation may cause local spider extinction in small habitat fragments (Miyashita et al. 1998).

Spider diversity may, therefore, peak at intermediate levels of urbanization. A similar pattern has been described for butterflies along an urban gradient (Blair and Launer 1997). However, any further development that changes the habitat structure of the once-natural habitat fragments decreases spider diversity. In the Phoenix area, xeric yards support a higher diversity than mesic yards, which represent the same level of fragmentation plus more radical habitat alteration. These results are similar to what McIntyre and Hostetler (2001) described for bees (Apoidea) from the same area. These results suggest that although negative effects of urbanization on arthropod diversity may be mediated through both habitat fragmentation and al-

teration, habitat structure alteration has a greater effect on arthropod diversity. A comparison of agricultural field and mesic yards further supports the idea that land use alteration has a greater effect on spider communities than the reduction of area per se. In terms of water availability and habitat productivity, agricultural sites appear as much larger versions of mesic yards. In this case, area does not compensate for the desert habitat alteration, as spider diversity in crop fields is still as low as in mesic yards.

Since other studies on urbanization effects on spiders focused on habitat fragmentation, it is hard to draw conclusions about the partial effects of fragmentation vs. habitat structure alteration. Gibb and Hochuli (2002) found that spider diversity was not affected by forest patch size fragmented by urbanization, though community composition did change. Bolger et al. (2000) described different results for different sampling methods and seasons. Spider diversity in scrub patches decreased with fragmentation, although abundance increased. As recommended by Gibb and Hochuli (2002), future studies should incorporate effects of fragmentation and habitat structure/land use alteration to better understand the complex effects of urbanization on arthropod communities.

In central Arizona, future landscape planning should (1) favor xeric over mesic yards, as recommended by McIntyre and Hostetler (2001) concerning pollinator communities, and (2) incorporate large remnants of natural habitats within the urban core, since such remnants appear to retain rich arthropod communities.

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APPENDIX

A table showing spider families and the number of individuals sampled in six habitat types in the greater Phoenix area between April 1998 and March 2000 is available in ESA's Electronic Data Archive: *Ecological Archives* A014-003-A1.