

Control of arthropod abundance, richness, and composition in a heterogeneous desert city

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Abstract. There is a demand for mechanistic studies to explore underlying drivers behind observed patterns of biodiversity in urban areas. We describe a two-year field experiment in which we manipulated bottom-up (resource availability) and top-down (bird predation) forces on arthropod communities associated with a native plant, *Encelia farinosa*, across three land-use types—urban, desert remnant, and outlying natural desert—in the Phoenix metropolitan area, Arizona, USA. We monitored the trophic structure, richness, and similarity of the arthropod communities on these manipulated plants over a two-year period. We predicted that (1) increased water resources increase plant productivity, (2) increased productivity increases arthropod abundances, and (3) in the urban habitat, top-down forces are greater than in other habitats and limit arthropod abundances. We also predicted that urban remnant habitats are more similar to urban habitats in terms of arthropod richness and composition. Strong interannual differences due to an unusual cold and dry winter in the first year suppressed plant growth in all but urban habitats, and arthropod abundances in all habitats were severely reduced. In the following year, arthropod abundances in desert and remnant habitats were higher than in urban habitats. Water had positive effects on plant growth and arthropod abundance, but these water effects emerged through complex interactions with habitat type and the presence/absence of cages used to reduce bird predation. Plants grew larger in urban habitats, and phenology also differed between urban and desert habitats. The results from caging suggest that bird predation may not be as important in cities as previously thought, and that arthropods may retard plant growth. As expected, desert communities are strongly bottom-up regulated, but contrary to predictions, we did not find evidence for strong top-down control in the city. Remnant habitats were intermediate between desert and urban habitats in terms of diversity, richness, evenness, arthropod composition and phenology, with urban habitats generally lowest in terms of diversity, richness, and evenness. Our study shows that control of biodiversity is strongly altered in urban areas, influenced by subtle shifts in top-down and bottom-up controls that are often superseded by climatic variations and habitat type.

Key words: arthropods; bottom-up forces; composition; diversity; *Encelia farinosa*; Phoenix, Arizona, USA; plant growth; predation; productivity; trophic dynamics; urban biodiversity; urbanization.

INTRODUCTION

Today, more than half of the human population lives in cities, and this proportion is increasing (McGranahan et al. 2005). This makes urban areas the most rapidly expanding ecosystems on Earth, and has therefore attracted increased attention by ecologists and social scientists in the last decade (Grimm et al. 2008a). Urban developments drive global climate change and regional air and water pollution (Grimm et al. 2008b) and influence ecosystem processes (Chapin et al. 2002). These changes ultimately influence species diversity and community structure (Shochat et al. 2006), which, in turn, may affect ecosystem function (Chapin et al. 1997). It is therefore essential to understand how urbanization changes biodiversity and community structure.

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Whereas much attention has been directed towards descriptive studies of urban biodiversity, the underlying causes for observed changes remain poorly understood (Shochat et al. 2006). All species in biological communities interact via predation, parasitism, competition, or mutualisms, forming food webs. Urbanization likely alters these interactions causing changes in the trophic structure of food webs, ultimately influencing biodiversity (Faeth et al. 2005). In this paper we address how urbanization alters abundances, diversity, and composition of arthropod communities associated with a common native plant, *Encelia farinosa*, via changes in trophic dynamics.

Trophic dynamics within communities can be regulated by intrinsic forces such as top-down and bottom-up forces (Hairston et al. 1960, Rosenzweig 1971, White 1978, Oksanen et al. 1981). Bottom-up theory states that energy supply from the bottom of the food web limits the number of trophic levels, together with relative

efficiency of the consumers (e.g., Lindeman 1942). Top-down theory, on the other hand, states that consumers control the biomass of lower trophic levels, creating negative feedbacks between increases in consumer growth rates along productivity gradients and the biomass of resource populations (Hairston et al. 1960, Oksanen and Oksanen 2000). One of the major effects of urbanization is an increase in limiting resources (Grimm et al. 2008a). Thus, as a consequence of urbanization, productivity often increases in cities and becomes a bottom-up force, driving changes in population density, community structure, and diversity (Shochat et al. 2006).

If bottom-up regulation dominates a community, then more resources should lead to increased plant growth and higher herbivore abundances (e.g., Price and Hunter 2005). Predator exclusion experiments, however, have documented that avian (Holmes et al. 1979, Marquis and Whelan 1994, Floyd 1996, Gruner and Taylor 2006) and invertebrate (Spiller and Schoener 1994) predators can act as top-down regulators of herbivorous insect communities on perennial plants. Likewise, light, nutrients, and water, which influence plant productivity, nutritional chemistry, and allelochemistry, may induce significant bottom-up effects on herbivores and their predators (Price et al. 1980, Hunter and Schultz 1993, Stiling and Rossi 1996, 1997, Forkner and Hunter 2000). Thus, in a three-level food chain with top-down regulation, increased productivity should lead to increased plant growth, insignificant changes in herbivore abundance (because they are limited from above), and increased predator abundance (e.g., Power 1992). Due to indirect urbanization effects such as lower predation pressure (Blair 2004) and increased availability of resources (Shochat et al. 2004), birds are often more abundant in cities (Marzluff et al. 2001). Predation by birds may therefore be a structuring force on urban arthropod communities.

Top-down and bottom-up forces may be modulated by extrinsic factors such as environmental stress (Menge and Sutherland 1987), pollution (Gregg et al. 2003), and changes in local climate (Baker et al. 2002). Urbanization moderates environmental variables by buffering seasonal fluctuations in limiting resources (water, nutrients) (Faeth et al. 2005). This is particularly true for urban ecosystems where surrounding areas are subject to large fluctuations or severe climate events. In arid environments, for example, plants respond rapidly to pulses of precipitation by germinating from seeds stored in the soil (Noy-Meir 1973). In a city with continuous irrigation, high resource availability, and the urban heat island, flowering plants are available in all seasons, extending the breeding seasons for arthropods and birds (McIntyre 2000, Chace and Walsh 2006, Walker et al. 2009). In arid areas, cities may become islands of resources, buffered against environmental stresses (Shochat et al. 2006).

Complicating the picture of how top-down and bottom-up forces alter abundances in urban areas is the enormous habitat heterogeneity that is associated with cities (McKinney 2002, Cadenasso et al. 2007). Many cities are traditionally built upon productive heterogeneous patches of land, leading to naturally high productivity and plant diversity (Kühn et al. 2004). Planting of exotic species may additionally contribute to high plant diversity (Walker et al. 2009). In addition, the urban matrix consists of a patchwork of fragmented landscape types, ranging from highly industrialized lots to well-maintained parks and green space, as well as patches of remnant natural land surrounded by urban development. With the high heterogeneity and habitat diversity in cities, it is likely that top-down and bottom-up forces may vary spatially among land-use and habitat types.

In Sonoran Desert habitats, plant productivity is limited primarily by water availability (Ehleringer and Cook 1984, Comstock and Ehleringer 1986). Light is generally not limiting, and nutrients do not become limiting until water availability is well beyond ambient (Martin and Stabler 2002). Consequently plant productivity is comparatively higher in irrigated agricultural areas and well-watered mesic habitats within cities than in desert remnants and outlying, contiguous deserts. Even native Sonoran Desert or nonnative desert plants are generally much more productive in urban environments than in their natural habitats (Martin and Stabler 2002). This unanticipated outcome stems from human perceptions, values, and socioeconomic factors (Hope et al. 2003) that lead humans to increase water usage in xeriscapes to keep desert plants “green” and growing, especially during dry periods typically when desert plants are seasonally senescent (Martin et al. 2004). Clearly then, water availability is a key variable linked directly to plant productivity (Lambers et al. 1998). Hence, this is a factor we controlled and manipulated.

We performed a two-year field experiment in which we manipulated resource availability and bird predation in three replicates of two urban (remnant, urban) habitats and one wildland (desert) habitat, to determine the effects of bottom-up and top-down forces across habitat types on abundances, richness, and composition of associated arthropod communities (Fig. 1). To test bottom-up forces, we manipulated water availability, and then monitored plant growth, the resource of importance to plant arthropods. To test top-down control, we manipulated bird predation, an important top-down factor on plant arthropods. Because bottom-up/top-down regulation of abundances and diversity and composition can also vary depending on abiotic environmental factors (e.g., Menge and Sutherland 1987), we ascertained air temperature and precipitation to determine how these affect trophic dynamics in cities. Our general hypotheses were that (1) plants are water limited and would grow faster and larger with increased water availability (Martin and Stabler 2002) regardless

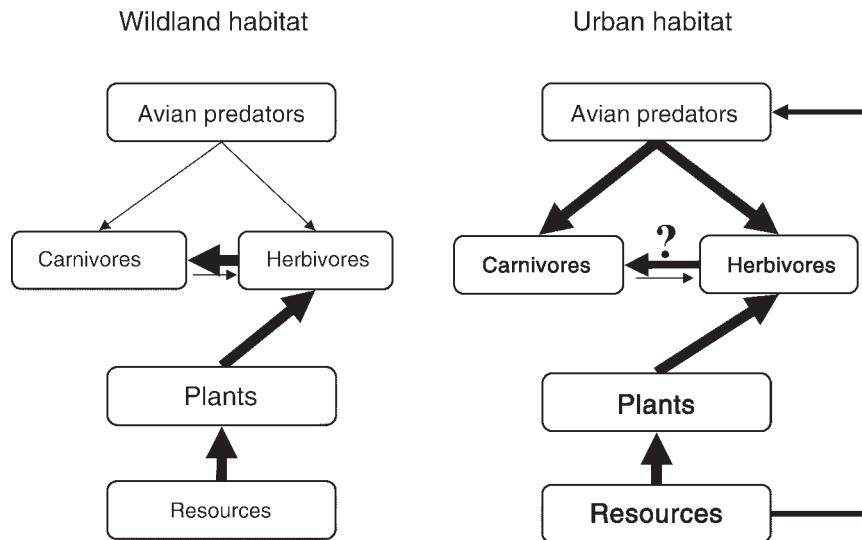


FIG. 1. Schematic depiction of proposed trophic dynamics in urban and wildland habitats (modified from Faeth et al. [2005]). In the wildland habitat (Sonoran Desert), trophic levels are limited by resources and are thus bottom-up controlled. Avian predation is limited. In the urban habitat (Phoenix, Arizona, USA, area), increased resources stimulate increase in biomass at higher trophic levels, but avian predation on arthropods combines with the bottom-up forces to control the trophic dynamics. The effect of carnivores on herbivores is uncertain. Bold fonts indicate greater relative biomass, and arrow width indicates the relative importance of the direct effect. The question mark indicates an unverified effect.

of habitat type. We also hypothesized that (2) deserts are bottom-up systems (Noy-Meir 1973, 1974), so that increases in plant growth associated with release of resource limitation by water would stimulate increases in the abundance of arthropods and changes in species composition (Crawford 1986). (3) Urban areas are under “joint control” of bottom-up and top-down forces where arthropod abundance increases with plant growth, but is simultaneously suppressed by predation by vertebrates, especially birds (Faeth et al. 2005). Here we predicted that arthropod abundances would increase on caged plants compared to uncaged plants if birds have a controlling effect on arthropods. Also, because of the proximity of remnant habitats to parks and residential yards with presumably similar air quality as other urban areas, we hypothesized that (4) plant growth and arthropod communities in remnant areas would be more similar to urban habitats than to desert habitats in terms of arthropod composition, richness, and evenness (Faeth et al. 2005).

METHODS

Study system

The Phoenix metropolitan area (Arizona, USA) is located in the Sonoran Desert (33°30' N, 112°10' W). Winter precipitation (December–March) averages by 82.5 mm (1954–2008; Phoenix Sky Harbor airport). Average annual air temperature is 22.7°C (1948–2007). Summers are hot, with maximum temperatures reaching 40–50°C, but winter temperatures have been as low as –8.3°C (1950). In the last few decades, however, winter

temperatures have rarely dropped below freezing for extended periods of time. January 2007 was the first time since 1990 that winter temperatures at Sky Harbor Airport were measured below 0°C. Local differences are common, thus we obtained climate data from one rural and one urban weather station (Arizona Meteorological Network; see map, Fig. 2).

To test bottom-up and top-down forces in different urban and rural settings, we chose nine sites for the manipulative experiments. Three desert sites were located in regional parks surrounding Phoenix (UP, WT and ES), three desert remnant sites were located within the city of Phoenix (DB and CS) or at the fringe of the city (SM), and three urban sites were located in human-altered landscapes, two of them located in elementary school yards (EX and ME) and one on the main campus of Arizona State University (SG; Fig. 2). Desert habitats were relatively open landscapes with native perennial vegetation. Remnant habitats were also open landscapes and contained similar vegetation as desert, however, the two remnant habitats in the city were also close to nonnative trees (e.g., *Eucalyptus* sp., *Rhus lancea*). The urban habitats were close to buildings and ornamental vegetation, most nonnative to Arizona.

For our study we chose brittlebush, *Encelia farinosa* (Gray) (Asteraceae), a native perennial shrub growing on uplands throughout the Sonoran and Mohave Deserts (Tesky 1993, Koehler 2003). Brittlebush is well known in studies of plant ecophysiology (e.g., Ehleringer 1982, Ehleringer and Cook 1990, Kunze et al. 1995, Nobel et al. 1998, Sandquist and Ehleringer 2003), and is used extensively as an ornamental plant in the Phoenix area

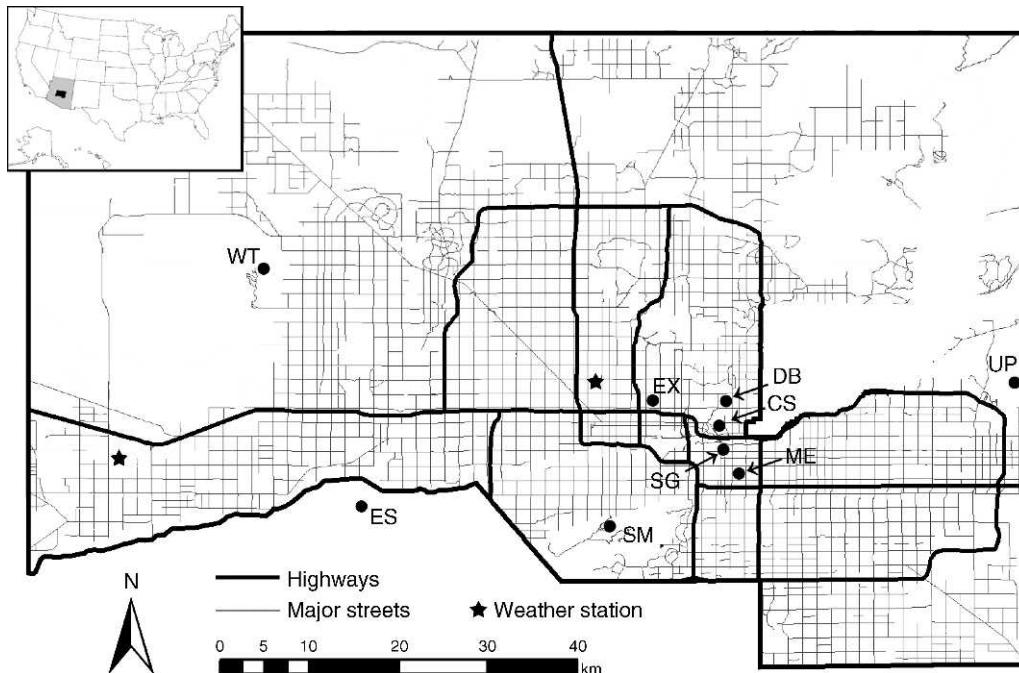


FIG. 2. Map of the Phoenix metropolitan area, with approximate location of the two weather stations (one rural, one urban) and the nine field sites: three desert sites in regional parks (UP, UT, and EX) surrounding Phoenix; three desert-remnant sites within the city of Phoenix (DB and CS) or at the fringe of the city (SM); and three urban sites (EX, ME, and SG).

in both xeric and mesic landscaping. Irrigated, it easily reaches 120 cm in height and width. The arthropod community on brittlebush is diverse (Marussich and Faeth 2009). Brittlebush thus provides a tractable system to quantify the fingerprint of urbanization on desert arthropod communities.

Bird predation may be frequent since common birds in the area (Cactus Wren *Campylorhynchus brunneicapillus* and Verdin *Auriparus flaviceps*), have been observed foraging for insects directly from brittlebushes (C. Bang, *personal observation*). The common Anna's Hummingbird (*Calypte anna*) is also known to have insect foraging as an essential part of its activity budget (Stiles 1971, Lyon et al. 1977).

Experimental setup

On each site, 60 brittlebushes in five-gallon (~18.9-L) pots were spread out in a grid-like pattern, with 0.8–2.0 m between each plant. The different sites varied in area (UP ~ 240 m², ES ~244 m², WT ~120 m², SM ~303 m², CS ~80 m², DB ~297 m², ME ~96 m², EX ~254 m², and SG ~72 m², constrained by fences or buildings). The setup can be described as a split-plot design with habitat type as plots and all the other treatments completely randomized within each plot and replicated three times, for a total of 540 plants. The plants were obtained from local nurseries (seeds collected locally, all plants approximately seven months old). Plants were placed in the field in October–November each year to facilitate invertebrate establishment prior to first sam-

pling in December. Half of the plants were enclosed in bird netting to exclude birds and other potential predators larger than the 1.9-cm mesh size. A cage consisted of three plant stakes positioned as an upside down cone enclosed with bird netting (Appendix: Fig. A1). The plants received three different water treatments; low, medium, and high (levels determined in a trial season of 2006). Each plant received 2 L supplemental water for 30 min at 06:00 hours and 14:00 hours two times a week (low), four times per week (medium), and daily (high). Total supplemented water for 6 months was thus approximately low, 192 L; medium, 384 L; and high, 672 L. All the pots had drain holes, so the soil never remained saturated. Ambient precipitation per pot was calculated using pot diameter and millimeters of precipitation; however, the supplemented water by far exceeded ambient precipitation both years. The plants were grown in pots (insulated, to moderate root temperatures of all plants since they were aboveground) to exclude confounding effects of soil types in the desert vs. the urban area. The pots contained soil consisting of ¼ native top soil and ¾ composted mulch, and two tablespoons (~29.6 mL) of Osmocote 18-6-12 N-P-K slow-release fertilizer (Scotts Miracle-Gro Company, Marysville, Ohio, USA) to maintain a sufficient soil nutrient level the first year. The plants were ~7 months old, averaging 43.6 ± 11.2 cm in height (mean ± SD) and 61.4 ± 26.7 g in dry mass (estimated). In the second year, we reused most of the plants and redistributed them randomly within the sites. Most of

the plants were therefore older and taller the second year (57.1 ± 20.3 cm, dry mass 139.2 ± 93.6 g) and had a lower growth potential due to possible early root binding, reproductive maturity, and less nutrients in the pot. Plant dry mass was estimated by measuring height and diameter monthly and compared to an equation developed from 360 plants from a trial season in 2006 (see Bang et al. 2010).

All desert and remnant sites were enclosed with poultry-netting fences to keep rabbits, ground squirrels, and deer from feeding on the plants or chewing on the irrigation lines. All sites were visited once a week and fence and irrigation lines inspected. December through April is the optimal growing season for brittlebushes, and consequently the period for highest arthropod activity (Marussich and Faeth 2009). Arthropods were therefore sampled monthly from December to May using a Vortis Insect Suction Sampler (Burkhard Manufacturing Company, Rickmansworth, UK) applied to each plant for 10 s, covering ~60% of the outer foliage. This removes a standardized sample of the arthropod community inhabiting the plant, allowing remaining individuals to reestablish until next month. The arthropods were identified to family level and then further separated into morphospecies, and categorized into general feeding guilds based on various sources (e.g., Borror et al. 1989, Bartlett 2005). Taxa, guild, and occurrence are listed in the Appendix (Table A3). Herbivore damage was not systematically measured, but flowering phenology and pollinators were measured in a separate study (Neil 2008).

Statistical analyses

Plant growth was controlled for initial differences by subtracting biomass measured the first month (December) from all subsequent monthly measures; thus, we analyzed observed change in dry mass for five months per season. To avoid negative values for logarithm transformation, the absolute value of the lowest negative value was added to all measures. These data were then tested for normality and homogeneity of variance using normal probability plots and residual scatter plots from a general linear model. As most of these data violated assumptions for parametric testing (normality and homogeneity of variance), the values were \log_e -transformed. The two years were analyzed separately using repeated-measures analysis of variance (rmANOVA) with site nested in habitat as a random variable to reduce the mean square error. We used PROC GLM and PROC MIXED in SAS 9.2 (SAS Institute 2008), using an autoregressive covariance structure on full models with all interactions. The random effects are not discussed below, but can be found in the ANOVA tables (Appendix: Table A2). For post hoc pairwise comparisons, we used *t* tests with Tukey-Kramer adjusted *P* values on least square mean (lsmeans) values. Similar repeated-measures analyses were applied to arthropod abundance, herbivore abundance and arthropod rich-

ness for six months per year. Effect sizes and figures are given in untransformed form.

A different approach was used for predatory arthropods (hereafter termed “carnivores”), which were not found on many plants, resulting in many zero samples. For carnivores, we therefore analyzed presence-absence data using generalized estimating equations (GEE) using PROC GENMOD in SAS 9.2 (SAS Institute 2008) for binary data with the logit link function and an autoregressive covariance structure. Post hoc pairwise comparisons were based on least-square means.

The experiment was balanced and the sampling effort was equal at all sites, hence we relied on taxon richness and evenness measures instead of using common diversity indices. However, to compare communities with different numbers of individuals, we used rarefaction and compared the habitats at the highest common sample size (Gotelli and Colwell 2001). To test composition and evenness in the different habitats, the arthropod taxa were ranked by abundance, then alphabetically. The length of the rank abundance curve gives a direct measure of family richness, and by taking the log of the proportion and the rank, the linear slopes give an indication of evenness (maximum evenness is 0). These slopes were tested with analysis of covariance (ANCOVA) using PROC REG and PROC GLM with Tukey-Kramer adjusted *P* values for post hoc tests in SAS (SAS Institute 2008). We supplemented the evenness measure with the Buzas-Gibson index $E = e^H/S$ (*H* is Shannon’s diversity index, *S* is the number of species) where perfect evenness is 1, and the rarefied Hurlbert’s probability of interspecific encounter (PIE), where perfect evenness also is 1 (Hurlbert 1971, Olszewski 2004).

Nonmetric multidimensional scaling (NMS) was used to ordinate the arthropod communities using Bray-Curtis distance to get a visual impression of arthropod community composition. To find out which families primarily accounted for the observed differences in arthropod assemblages, we analyzed the difference percentage using SIMPER (Clarke 1993). This analysis identifies taxa typical of a specific environmental type and gives a measure of the observed difference. For rarefaction, ordination, and nonparametric tests we used PAST version 1.97 (Hammer et al. 2001), ECOSIM (Gotelli and Entsminger 2009), and EstimateS Win 8.20 (Colwell 2006).

RESULTS

Temperature and precipitation

Climate varied between the urban and rural habitats over the two-year experiment (Appendix: Table A1). The rural weather station measured 21 days below freezing with minimum temperature -5.6°C , while the urban station measured eight days below freezing, same minimum temperature (November 2006–March 2007). The following year, rural areas experienced 16 days below freezing, minimum temperature -2.9°C , while

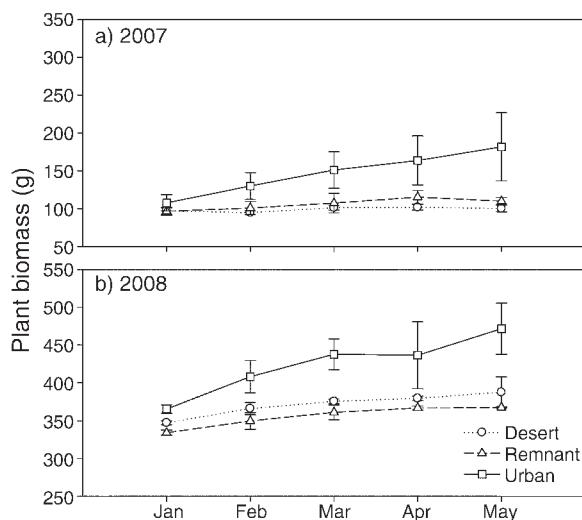


FIG. 3. Growth of brittlebush plants, *Encelia farinosa*, in (a) 2007 and (b) 2008 in three different habitats. The January measure is accumulated biomass since December. Data are means \pm SE. The biomass was overall higher in 2008 because the plants were reused from 2007 after randomization (note the different scales on the y-axes).

urban areas had 13 days below freezing, same minimum temperature. While the average temperature was relatively similar between the two stations, the average minimum temperature was 0.9°C higher in urban than rural areas both years. The amount of precipitation was 42.4 mm (\sim 2.3 L/pot) at the rural station and 63.5 mm (\sim 3.4 L/pot) at the urban station (November 2006–May 2007). The following year the rural area received 93.5 mm (\sim 5.0 L/pot) and the urban area received 141.2 mm (\sim 7.5 L/pot, November 2007–May 2008). Thus, the first year was cold and dry, whereas the second year was warmer with more rain.

Plant growth

Plants in urban habitats grew larger than their rural counterparts and experienced faster recovery from plant damage due to the unusual frost in 2007. Plants in all habitats experienced frost damage in January, killing 45% of the desert plants, 43% of the remnant plants, and 5.6% of the urban plants. The dead plants were replaced by similar-sized plants to maintain sample sizes as consistent and equal as possible. By the end of the season, plants on higher water levels had higher growth by an average of 3.6 g between low and medium and 5.5 g between low and high water levels ($F_{2,2525} = 6.43$, $P = 0.0016$; t test: low and medium $t = -2.39$, Tukey-Kramer adjusted $P = 0.0448$ and low and high $t = 3.52$, $P = 0.0013$). Water, cage, and month affected plant growth differently in the three habitats in 2007. On average, desert plants peaked at medium water levels, while remnant and urban plants peaked at high water levels (water \times habitat effect, $F_{4,2525} = 3.96$, $P = 0.0033$). There was an overall negative effect of cages on plant growth,

although the difference between the means was small (uncaged, 117.6 ± 14.0 g [mean \pm SE], caged, 115.0 ± 14.1 g; $F_{1,2525} = 3.86$, $P = 0.0495$). Plants in the urban habitat increased in biomass on average 16.3 g per month, whereas desert (0.81 g/month) and remnant (3.4 g/month) plants barely returned to initial biomass after the frost event (habitat \times month effect, $F_{8,2525} = 21.23$; $P < 0.0001$, Fig. 3a). The trajectories show differences in phenologies among the habitats, with desert plants peaking in March, remnant plants in April, and urban plants continuing to increase in May. The continuing growth in May was associated with high water availability, as plants with medium and low water availability essentially stopped growing from March to May (water \times month effect, $F_{8,2525} = 2.59$, $P = 0.0082$). In May, plants with high water availability were on average 16.9 g larger than those at low water treatment (post hoc t test, $t = 4.87$, Tukey-Kramer adjusted $P = 0.0001$).

Habitat was a strong predictor for plant growth in 2008, with an average of 65.2 g more dry mass per plant in urban habitats than for remnant plants ($F_{2,6} = 6.29$, $P = 0.0336$; t test, $t = -3.41$, Tukey-Kramer adjusted $P = 0.0331$). Caged plants grew on average 11.6 g larger than uncaged plants ($F_{1,2580} = 15.95$, $P < 0.0001$). Rates of plant growth were greater in urban (26.5 g/month) than in desert (10.1 g/month) and remnant habitats (8.4 g/month, habitat \times month effect, $F_{8,2580} = 4.91$, $P < 0.0001$; Fig. 3b). At one of the urban locations (EX), many plants reached maximum height (23% $>$ 120 cm). Plants in desert and remnant habitats increased with water availability, whereas the opposite took place in urban habitats, suggesting that urban plants had reached maturity by the end of the second season (habitat \times water effect, $F_{4,2580} = 6.02$, $P < 0.0001$). A cage \times water effect was driven by plants with high water availability gaining 23.5 g more than uncaged, high water plants (cage \times water effect, $F_{2,2580} = 4.79$, $P = 0.0083$; $t = -4.50$, Tukey-Kramer adjusted $P = 0.0001$). This effect was, however, noteworthy only in the urban habitat (habitat \times cage \times water effect, $F_{6,2580} = 5.26$, $P = 0.0003$). Water as a main factor was not significant in 2008.

Arthropod abundance

The 9573 specimens were identified to 203 morpho-species (or 9275 specimens to 93 families, Appendix: Table A3). Total abundance was lower in desert and remnant habitats in 2007 than in 2008 (Table 1).

In 2007 overall arthropod abundance was greater with increased water ($F_{2,3064} = 3.45$, $P = 0.0320$). There were no main effects of habitat or cages (Appendix: Table A2.3). Abundance varied with time as expected because arthropods follow the phenology of the plants. Abundances demonstrated a different trajectory on desert plants than on remnant and urban plants (habitat \times month effect, $F_{10,3066} = 8.73$, $P < 0.0001$; Fig. 4a). Abundance in the desert was lowest among the habitats in February, but highest in April. Cage treatment and water availability interacted with each other and with

TABLE 1. Community measures for arthropods sampled from 180 brittlebushes per habitat, monthly from December to May, identified to morphospecies.

Habitat and morphospecies	Abundance		Richness		Diversity (rarefaction \pm SD)		Evenness† ($e^{H/S}$)	
	2007	2008	2007	2008	2007‡	2008‡	2007	2008
Desert	830	2325	111	108	110.65 \pm 0.58	91.42 \pm 3.27	0.463	0.163
Herbivores	546	1656	51	49				
Carnivores	120	327	23	27				
Remnant	1069	2794	101	95	91.28 \pm 2.82	76.66 \pm 3.28	0.240	0.070
Herbivores	648	2352	49	44				
Carnivores	128	214	26	21				
Urban	1084§	1471	97	75	87.68 \pm 2.64	74.86 \pm 0.37	0.250	0.116
Herbivores	850§	1196	53	31				
Carnivores	64§	70	19	18				

Notes: By “carnivores” we refer to predatory arthropods. Rarefied diversity is compared at maximum common sample size. See *Diversity and evenness* for measures on family.

† E is the notation for evenness of the Buzas-Gibson index; H is Shannon’s diversity index; S is the number of species.

‡ In 2007, 830 samples; in 2008, 1470 samples.

§ The February sample is missing from one location.

habitat to affect arthropod abundances ($F_{4,3064} = 4.21$, $P = 0.0021$). In urban and remnant habitats, arthropods became more abundant on uncaged plants with increased water availability (low to high: remnant, 99%; urban, 123%), but arthropods on caged plants decreased (remnant, -16% ; urban, -33%). In the desert, the effect was the opposite (uncaged, -9% ; caged, 73%).

In 2008 uncaged plants had more arthropods per plant than did caged plants ($F_{1,3126} = 20.89$, $P < 0.0001$; Appendix Table A2.4). Uncaged plants in desert and urban habitats had on average 54% and 66% more arthropods than caged plants (desert and urban, respectively; habitat \times cage effect, $F_{2,3126} = 5.47$, $P = 0.0042$; $t = 4.01$, Tukey-Kramer adjusted $P = 0.0009$ and $t = 3.97$, $P = 0.0010$). Arthropod abundance in the desert peaked in March while remnant and urban habitats peaked in April, with on average 18% higher abundances in remnant than urban habitats (habitat \times month effect, $F_{10,3126} = 10.47$, $P < 0.0001$; Fig. 4b). In 2008, water availability did not have any direct effect on arthropod abundance.

Herbivore abundance

As the majority of the arthropods were herbivores, factors affecting herbivore abundance were similar to those affecting total arthropod abundance (e.g., Fig. 4). Herbivore abundance increased with water availability in 2007 ($F_{2,3066} = 3.13$, $P < 0.0438$). Month was significant as expected because herbivores track the greening and flowering of the plants. Desert herbivores followed a different trajectory than urban and remnant herbivores (habitat \times month effect, $F_{10,3068} = 9.71$, $P < 0.0001$). Herbivore abundance in the desert was lowest among the habitats in February, but highest in May. Herbivores on uncaged plants generally increased in abundance with increased water availability, while the ones on caged plants did not respond to water treatments ($F_{2,3066} = 3.51$, $P = 0.0299$). In urban and remnant habitats, herbivores on uncaged plants in-

creased in abundance with increasing water treatment (low to high; remnant, 130%; urban, 151%), but on caged plants they decreased with increasing water (remnant, -21% ; urban, -38% ; $F_{4,3066} = 3.91$, $P = 0.0036$). In the desert habitat, the trend was the opposite (uncaged -6% ; caged 118%). The negative effect of cages on herbivore abundance was greatest at high water availability in urban habitats (t test, $t = 3.96$, Tukey-Kramer adjusted $P = 0.0094$).

Similar to total arthropods, water availability did not have any effect on herbivore abundance in 2008 (Appendix: Table A2.6). Cages, however, reduced herbivore abundance by 2% ($F_{1,3126} = 14.81$, $P = 0.0001$). This pattern was prominent in desert (15%) and urban (12%), but not in remnant (-3%) habitats

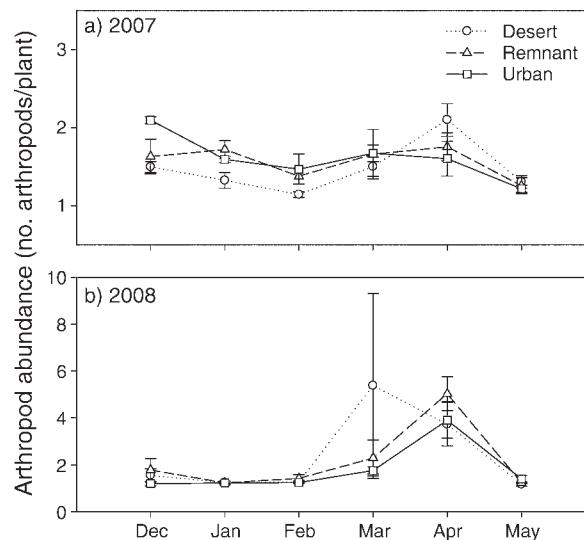


FIG. 4. Arthropod abundance per brittlebush plant in (a) 2007 and (b) 2008 in three different habitats. Plot size varies (see *Methods: Experimental setup*). Data are means \pm SE. Notice the different scales on the y-axes.

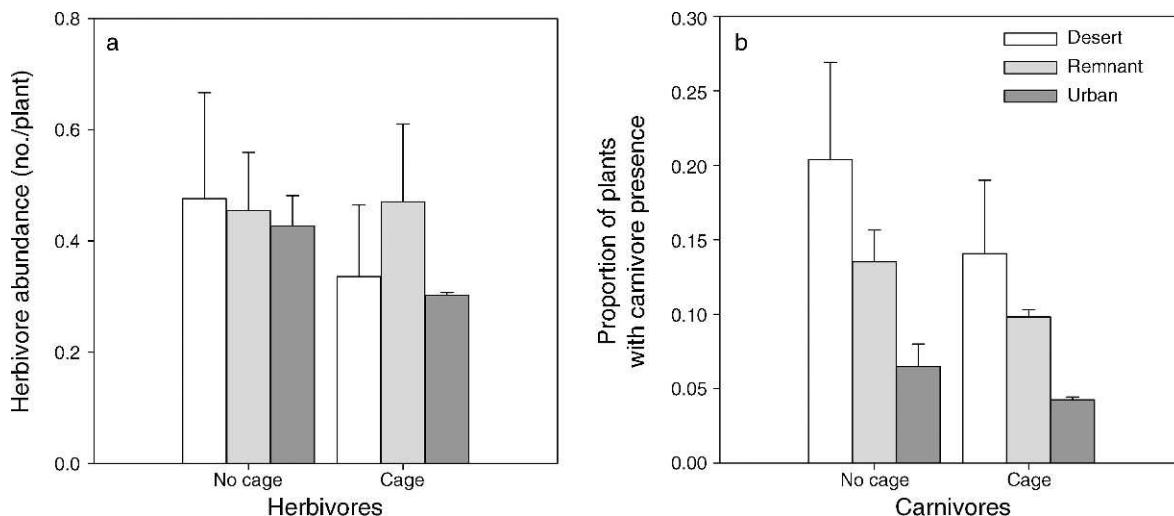


FIG. 5. Effect of cages on (a) herbivore abundance per brittlebush plant and (b) carnivore presence in 2008. Data are means + SE.

(habitat \times cage effect, $F_{2,3126} = 5.31$, $P = 0.0050$; desert $t = 3.76$, Tukey-Kramer adjusted $P = 0.0024$ and urban $t = 3.34$, $P = 0.0110$; Fig. 5a). Herbivore abundance in the desert increased faster in March, while remnant and urban habitats shared similar trajectories, with on average 14% higher abundances in remnant habitats than urban. Abundances in March, however, showed considerable variation among the desert sites (habitat \times month effect, $F_{10,3126} = 11.67$, $P < 0.0001$).

Carnivore presence

The most important carnivore pattern in 2007 was the large difference between habitats. Neither cage nor water had any effect on carnivore presence. The full GEE (generalized estimating equations) model did not converge (not enough data to properly estimate the binomial probability structure). Thus, we based our analyses on a model with 13 factors plus the random factor (excluding the four-way and the habitat \times water \times month effects). The GEE analysis on carnivore presence revealed strong habitat effects in 2007, regardless of time ($\chi^2 = 24.50$, $P < 0.0001$, Appendix: Table A2.7, habitat \times month effect, $\chi^2 = 12.82$, $P = 0.2338$). In urban habitats 24.4% of the plants had carnivores present compared to remnant (46.7%) and desert (46.7%) habitats (urban vs. remnant, $\chi^2 = 19.72$, $P < 0.0001$; urban vs. desert, $\chi^2 = 19.31$, $P < 0.0001$).

A model with 12 factors plus random factor (further excluding the habitat \times cage \times month effect) also revealed strong habitat effects on carnivore presence in 2008, where only 5.4% of the plants in urban habitats had carnivores present compared to remnant (11.7%) and desert (17.2%) (habitat effect, $\chi^2 = 26.18$, $P < 0.0001$; Appendix: Table A2.8; urban vs. remnant, $\chi^2 = 23.29$, $P < 0.0001$; urban vs. desert $\chi^2 = 29.56$, $P < 0.0001$). Caged plants had 30.3% lower frequency of carnivore presence than uncaged plants (cage effect, $\chi^2 =$

7.18, $P = 0.0074$; Fig. 5b). Carnivores appeared on plants earlier in the desert than in remnant and urban habitats (habitat \times month effect, $\chi^2 = 23.86$, $P = 0.0080$). Carnivores on uncaged plants increased in frequency by 30% from low to high water availability, whereas carnivores on caged plants peaked at medium water availability (cage effect, $\chi^2 = 6.40$, $P = 0.0407$).

Arthropod richness

Whereas water affected arthropod abundance in 2007, it did not affect arthropod (morphospecies) richness per plant (Appendix: Table A2.9). Uncaged plants, however, had on average 11% higher arthropod richness than caged plants ($F_{1,3064} = 5.04$, $P = 0.0248$). Richness followed similar trajectories as abundance in 2007, as arthropod richness in the desert was lowest among the habitats in February (0.18 species per plant) and highest in April (1.37 species per plant; habitat \times month effect, $F_{10,3066} = 7.40$, $P < 0.0001$). Similar to arthropod abundance the same year, arthropods on uncaged plants increased in richness with increasing water treatment and then decreased with increasing water on caged plants in urban and remnant habitats ($F_{4,3064} = 3.55$, $P = 0.0068$). For example, in remnant habitats, richness on uncaged plants at low water availability was on average 0.67 per plant, compared to 0.86 on uncaged plants at high water availability ($t = 4.02$, Tukey-Kramer adjusted $P = 0.0075$). This effect was greatest at high water availability in urban habitats as uncaged plants had 0.35 more taxa than caged plants ($t = 3.70$, Tukey-Kramer adjusted $P = 0.0248$).

Water did not affect richness in 2008. The cage treatment, however, reduced arthropod richness by 25% ($F_{1,3126} = 29.52$, $P < 0.0001$; Appendix: Table A2.10). This difference continued throughout the year (cage \times month effect, $F_{5,3174} = 2.53$, $P = 0.0270$). Similar to abundance, desert arthropods increased in richness

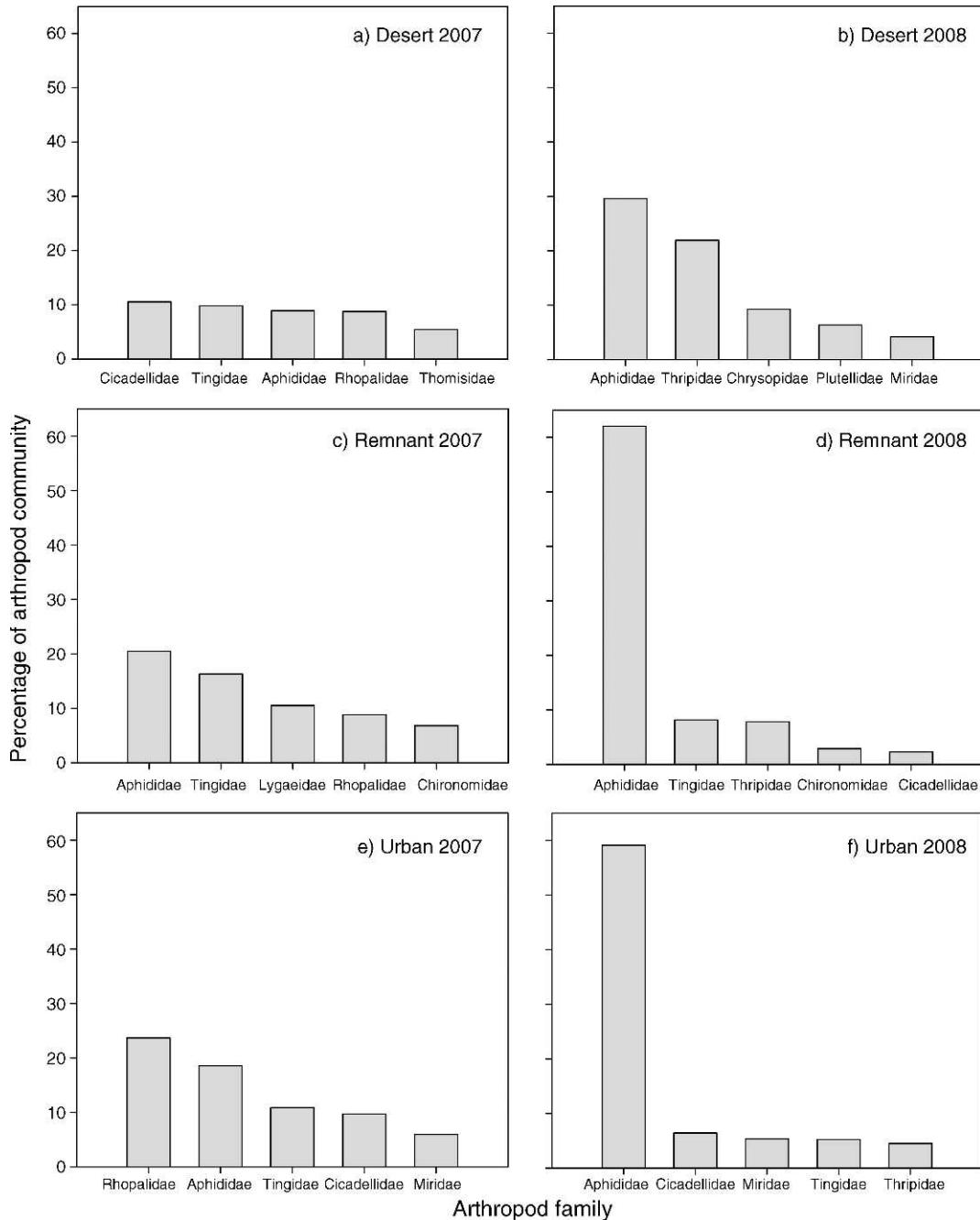


FIG. 6. Top five arthropod families in three habitats in 2007 and 2008. The arthropods were collected from 540 brittlebushes (*Encelia farinosa*, Asteraceae) over six months (December–May) each year.

faster than in the other habitats, and urban habitats had the lowest richness per plant (urban, 0.63; remnant, 0.80; desert, 0.95; habitat \times month effect, $F_{10,3126} = 8.98$, $P < 0.0001$).

Arthropod composition

In 2007, arthropod family composition varied between the habitats (Fig. 6, left-hand panels). Desert

habitats (Fig. 6a) had, in rank order, the dominant families Cicadellidae (10.56%), Tingidae (9.80%), Aphididae (8.91%), and Rhopalidae (8.78%). Whereas these four families are all major herbivore families, the fifth dominant family was the predator family Thomisidae (5.47%). Abundant families in remnant areas (Fig. 6c) were Aphididae (20.49%), Tingidae (16.32%), Lygaeidae (10.53%), Rhopalidae (8.82%), and Chironomidae



PLATE 1. Aphids are urban adapters—the arthropod equivalent to pigeons, starlings, and sparrows. Photo credit: C. Bang.

(6.83%). Thomisidae was ranked 6th (3.13%). For comparison, Chironomidae were only found once in the desert (ranked 54th). The most abundant families in the urban habitat (Fig. 6e) were Rhopalidae (23.68%), Aphididae (18.58%; see Plate 1), Tingidae (10.88%), Cicadellidae (9.72%), and Miridae (5.97%). Here, Thomisidae and Chironomidae (1.06%) were ranked as 12th and 16th, respectively. The predator families Thomisidae and Chrysopidae (10th) shared the same rank space, with 1.35% each.

In 2008 all the habitats were dominated by Aphididae, but great differences were found among the habitats (Fig. 6, right-hand panels). In the desert (Fig. 6b) Aphididae comprised 29.6% of the samples, followed by Thripidae (21.95%), Chrysopidae (9.24%), Plutellidae (6.35%), and Miridae (4.19%). Again, a predator family was ranked among the top five families in the desert (Chrysopidae). In the remnant habitat (Fig. 6d), the dominant families were Aphididae (62.03%), Tingidae (8.15%), Thripidae (7.83%), Chironomidae (2.88%), and Cicadellidae (2.27%). In urban habitats (Fig. 6f) Aphididae (59.15%), Cicadellidae (6.43%), Miridae (5.37%), Tingidae (5.23%), and Thripidae (4.52%) were the most abundant families.

Diversity and evenness

For both richness and rarefied richness, diversity was higher in the desert for both years, whereas urban habitats had the lowest diversity (Table 1). Evenness was highest in desert and lowest in urban habitats, whereas remnant habitats were intermediate. This pattern was consistent at both taxonomic levels.

In addition to the calculated evenness measures (Table 1), analysis of covariance on the slopes of log-transformed ranks (of family abundance) indicates that evenness was higher in the desert and lowest in the urban habitat in 2007, as desert had a less steep slope than remnant and urban (ANCOVA, $F_{1,2} = 8.06$, $P = 0.0005$; $\beta_1 = -1.401$ vs. $\beta_1 = -1.622$ (remnant), Tukey-Kramer, $P < 0.0001$; $\beta_1 = -1.401$ vs. $\beta_1 = -1.675$ (urban), $P < 0.0001$). The urban slope was steeper than the remnant slope ($P = 0.0434$). In 2008 the desert community structure switched from an even to a less even community. Desert and remnant slopes were different (ANCOVA, $F_{1,2} = 1.91$, $P = 0.1516$; $\beta_1 = -1.835$ vs. $\beta_1 = -1.712$ (remnant), Tukey-Kramer, $P < 0.0001$; $\beta_1 = -1.835$ vs. $\beta_1 = -1.708$ (urban), $P = 0.0024$; remnant vs. urban $P = 0.3349$). Similar analyses were performed on morphospecies, but are not reported since the results were similar.

Since these slopes are dependent on species richness, expected evenness should be calculated at a standardized size, which is the purpose of rarefaction. Desert had higher evenness (of families) in 2007 than did remnant and urban (Hurlbert's PIE; desert, 0.949, 95% confidence interval [0.948–0.950]; remnant, 0.902 [0.897–0.908]; urban, 0.879 [0.873–0.885]; sample size 761). In 2008, desert maintained the highest evenness, whereas remnant had the lowest evenness (desert, 0.846 [0.838–0.854]; remnant, 0.597 [0.575–0.618]; urban, 0.637 [0.632–0.641]; sample size 1381).

Similarity

Urban arthropod communities were clearly dissimilar from desert arthropod communities, with remnant

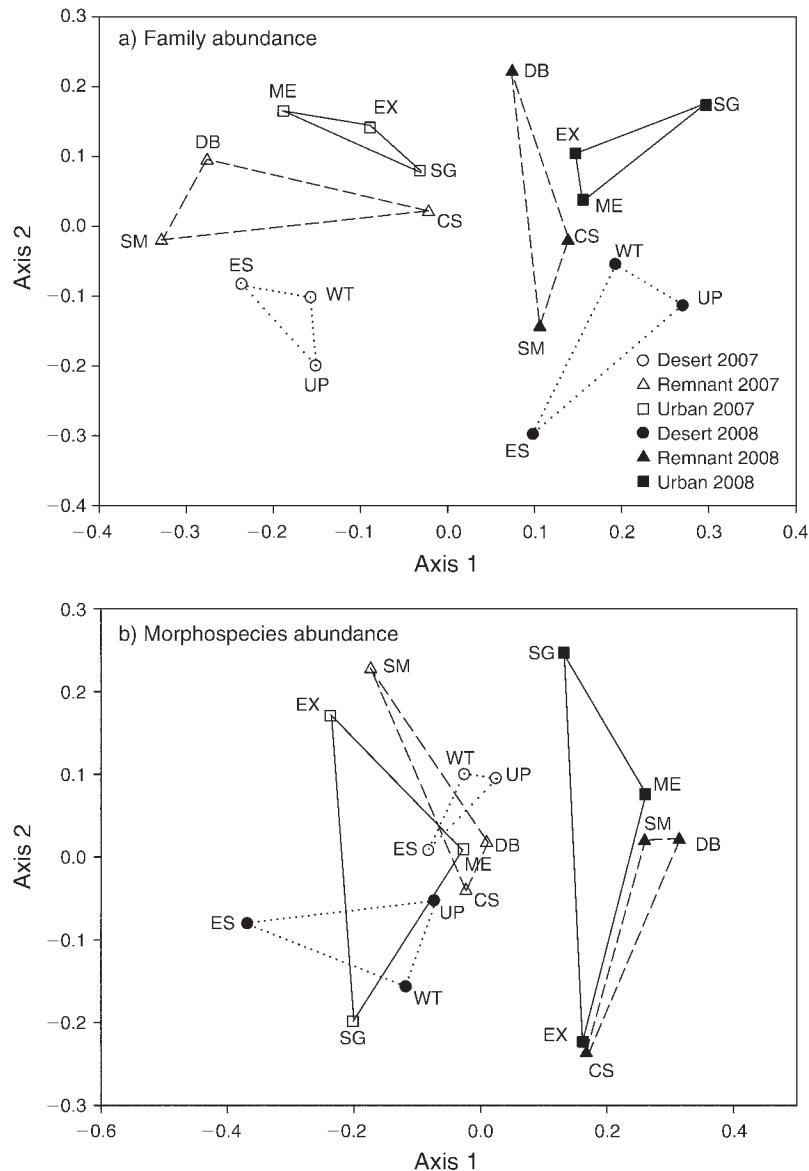


FIG. 7. Nonmetric multidimensional scaling of log-transformed ($\log_{10}[n + 1]$) arthropod (a) family abundances and (b) morphospecies abundances in nine locations in 2007 and 2008 based on Bray-Curtis distance. For (a) family abundances, stress = 0.255; axis 1 explains 52.8% of the variation and axis 2 explains 14.0%. For (b) morphospecies abundances, stress = 0.300; axis 1 explains 37.9% of the morphospecies variation, and axis 2 explains 14.5%. For the habitat site key, see the Fig. 2 legend.

habitats falling somewhere in between. Ordination of the families gave the clearest results (Fig. 7a), but ordination of morphospecies was also informative, since the desert communities for 2008 almost overlapped with the 2007 samples (Fig. 7b).

A difference of >40% in arthropod composition was observed between desert and urban habitats, whereas the smallest difference was between desert and remnant habitats (38%, SIMPER analysis; Table 2). This pattern was similar for both years, but the arthropod families that contributed to these differences varied. It was not always the dominant group that contributed to the major differences. For example, Braconidae (a parasit-

oid wasp) was ranked 8th in urban habitats in 2007, whereas the fruit fly family Tephritidae was ranked 7th in the desert, and the spider families Dictynidae and Araneidae were ranked 9th and 11th, respectively, in remnant habitats in 2008.

DISCUSSION

It has been a long-standing goal for ecologists to determine whether structure and diversity in biological communities are imposed by resources and competition (bottom-up) or predation, disease, or parasitism (top-down) (e.g., Hairston et al. 1960, Menge and Sutherland 1976, 1987, Leibold 1989, Hairston and Hairston 1993).

TABLE 2. Results of SIMPER analysis between arthropod family compositions in the three different habitats based on Bray-Curtis distance.

Habitat	Difference (%)	Shared families (%)	Contribution of similarity†	
			Contributing family (%)	Contributing family (%)
2007				
Desert vs. remnant	38.41	40	Aphididae (remnant, 1.613)	Chironomidae (remnant, 1.602)
Desert vs. urban	41.08	35	Aphididae (urban, 1.718)	Braconidae (urban, 1.427)
Remnant vs. urban	39.12	36	Miridae (urban, 1.553)	Chironomidae (remnant, 1.435)
2008				
Desert vs. remnant	37.86	38	Tingidae (remnant, 1.601)	Chironomidae (remnant, 1.526)
Desert vs. urban	40.79	38	Tephritidae (desert, 1.875)	Tingidae (urban, 1.506)
Remnant vs. urban	38.29	38	Dictynidae (remnant, 1.661)	Araneidae (remnant, 1.441)

† Only the two most important contributing families are listed.

Although these forces have been explored in many natural and agroecosystems, they are not well understood in urban areas. Understanding the relative importance of these forces is the key to unlocking how urbanization alters abundances, diversity, and composition of urban biological communities. In natural and agroecosystems studies, experiments controlling bottom-up and top-down forces are typically employed to test the relative importance of each to community diversity and trophic structure (e.g., Tilman and Downing 1994, Schmitz and Sokol-Hessner 2002). Yet, the equivalent experiments are very rare in urban ecological research. Here, we quantified the effects of predators (top-down) and water as a resource (bottom-up) on the relative abundance and richness of herbivorous and carnivorous arthropods, and ultimately on plant growth and biomass. More importantly, we were interested in exploring how these vary among urban, remnant, and natural desert sites within an urban-rural landscape patchwork. Our findings can be grouped broadly into four categories: strong interannual differences, strong effects of land use, strong but variable effects of water, and serendipitous cage effects, which practically reversed the experiment.

Strong interannual differences

Weather had a major impact on our results. In addition to limiting plant growth, unusually cold weather in 2007 also likely affected arthropod abundance and richness directly, as abundance remained relatively low throughout the year. The most dominant group in our study, aphids, is sensitive to cold temperatures and can be killed by just a few hours below the freezing point (Bale et al. 1988). If lower temperature limitations are relaxed, however, then aphids have the potential to increase quickly in population size (Hazell et al. 2010), as evidenced in all habitats the second year of this study.

Strong effects of land use

Habitat type had strong effects on plant growth and arthropod richness and abundance. Although urban

habitats also suffered some frost damage and reduced arthropod abundance, interannual variation was strongly damped. The urban heat island has previously been credited for increased plant survival in cities during cold winters (Baker et al. 2002), and increased minimum temperature could explain the rapid recovery of urban plants after the frost event. However, urban plant growth was also significantly better the second year, when the differences in minimum temperatures were less pronounced. Because plants in all habitats received the same levels of water and nutrients, the reason for the difference in plant growth must have been due to characteristics of the habitat itself. We suggest that sheltering effects of the built structures in urban habitats contribute to more favorable growth conditions. This led us to test the effects of wind speed on plant growth in cities (Bang et al. 2010), where reduced wind speed led to increased plant growth in cities.

Although much of the difference in plant growth may be explained by the sheltering factors, the habitat effects played out differently through various interactions. In many cases, habitat effects were expressed as differences in phenology (habitat \times month effect). The timing of peak growth, peak abundance, and peak richness differed between desert habitats and urban habitats, with remnant habitats either intermediate or more similar to urban habitats. The habitat effect was most pronounced in 2008, but the interaction effects with habitat were strong both years.

Strong, but variable, effects of water

As expected in a desert ecosystem, water had strong effects on plant growth, total arthropod abundance, and on abundance of herbivores. Water availability seemed to have the strongest effects in the dry year (2007), whereas in 2008 the effects of water were mediated through complex interactions with cage and habitat. Many of the plants at particularly one urban location reached maximum size during the second season, and signs of root binding were present. Productivity in urban habitats thus seemed not to be affected by water availability only. We suggest that water was not a

limiting factor for plant growth in urban habitats in 2008.

Serendipitous cage effects

Unintended cage effects allowed us to understand the role of arthropod predators rather than birds on trophic structure and plant growth. If predatory birds controlled arthropod abundances, then caged plants should have higher abundances of arthropods than uncaged plants. Instead, the opposite occurred. Unexpectedly, our cage design seemed to not only exclude birds but also deterred colonization of arthropods. The positive effects of caging on plant growth and unexpected negative effects on arthropod abundance (in 2008) suggest two mechanisms, or more likely, a combination of them. First, the cage design provided stabilization and protection against wind, thereby releasing the plant from mechanical stress and allowing the plant to accumulate more aboveground biomass (Cordero et al. 2007). Second, the increased abundance of herbivores on uncaged plants correlated with reduced plant biomass, whereas the herbivore-released caged plants correlated with higher plant biomass and fewer herbivores. We did not measure herbivore damage in this study, but insecticide-treated brittlebushes in a similar study revealed higher biomass when arthropods were removed, suggesting negative effects of invertebrate herbivory (J. L. Sabo, *unpublished data*). The reduced biomass on plants with more herbivores could be a direct effect of phloem and tissue consumption by herbivores, but may also be an indirect effect of the cost of induced plant resistance via secondary plant compounds or mechanical defenses that deter herbivory (Kunze et al. 1995, Karban and Baldwin 1997). Alternatively, the increased growth of caged plants may have deterred herbivores via increase in carbon-based defenses (Karbon and Baldwin 1997). Whatever the actual mechanisms, caged plants functionally became one-trophic-level systems (Power 1992), and uncaged plants became two- or three-trophic-level systems. Carnivores occurred more often on uncaged plants, without any obvious negative effects on herbivore abundance. This might suggest that carnivores respond to herbivores (bottom-up) rather than controlling them (top-down). Thus, the unexpected cage effect suggests impacts of herbivorous arthropods on plant growth, while our question about bird predation effects remains unresolved (Fig. 1).

Bottom-up or top-down?

Our initial goal was to examine bottom-up and top-down forces in habitats with different urban settings. The effects of water (bottom-up) and arthropod predators (top-down), however, were subtle. In most cases they were overridden by climate and habitat type and mediated through complex interactions with cage and habitats.

If desert ecosystems are controlled from the bottom up, then improved plant growth and water availability should stimulate an increase in arthropod abundance as well (herbivores and carnivores) (Crawford 1986). This prediction was confirmed in the desert habitats where improved plant growth the second year was associated with increased arthropod abundance (both herbivores and carnivores). In the same vein, if urban systems exhibit strictly bottom-up control, we would expect to see higher abundances of arthropods on urban plants, because urban plants grew notably better. This prediction was not supported. Documenting strong top-down effects in terrestrial ecosystems has proven difficult in non-urban ecosystems (Strong 1992), due to differences among species within trophic levels or differences in species interactions in changing environments (Hunter and Price 1992). Low abundance of carnivores raises the question of whether the carnivores in our study comprised a functionally significant trophic level (*sensu* Murdoch 1966, Fretwell 1987, Power 1992). Controlling predatory arthropods in addition to birds and then measuring changes in herbivore abundance would be a way to test the effects of carnivorous vertebrates and invertebrates. Our results thus suggest that bottom-up forces are strong in the desert, whereas in urban habitats, bottom-up forces are weak, despite no evidence for strong top-down forces.

The proportion of two spider families differed between remnant and urban habitats in 2008. Carnivores have more efficient energy assimilation than most herbivores, and a low carnivore:herbivore ratio implies a slow energy turnover rate through the consumer pathway whereas a high ratio implies a rapid flow rate (Begon et al. 1996). The carnivore:herbivore ratio was very low in both remnant and urban habitats, and carnivores were generally more dominant in the desert than in remnant and urban habitats, indicating a shift in trophic dynamics. We suggest that predatory arthropods are more important for structuring the community in desert habitats than in urban habitats.

Arthropod composition and diversity

Diversity was lower in urban habitats than in desert habitats at both family and morphospecies levels. Interestingly, richness and diversity were lower in the presumably more favorable year (2008) in all habitats. Evenness, which is a component of diversity, was higher in desert than urban habitats, but also declined the second year. This supports previous research for birds—richness and evenness decline leading to biodiversity loss in urban areas (Shochat et al. 2010). Shochat et al. (2010) suggested that interspecific competition favoring synanthropic species (species associated with humans) is a structuring factor in urban ecosystems for birds. It is yet unclear if urban arthropod communities are structured by competition, and other factors may also influence diversity (e.g., species–area effects). The strong presence of aphids in urban environments, however,

suggests that they are urban adapters—the arthropod equivalent to pigeons, starlings, and sparrows.

*Remnant communities are intermediate
between urban and wildland*

Although the composition of arthropods changed between the two years, the relationships between the habitat categories remained similar. Remnant habitats are interesting because they are preserved habitats that mimic wildlands. They are also susceptible to fragmentation effects (e.g., obstruction of dispersal patterns, reproductive isolation, inflow of synanthropic species), as they become increasingly isolated as the city expands its boundaries (Collinge 1996, Pinheiro et al. 2006). In the Phoenix (Arizona, USA) metropolitan area, the distance from the city core to the urban fringe increased by one mile (~1.61 km) per year from 1990 to 1998 (Gober and Burns 2002). Our results show that richness, evenness, and composition (especially the dominance of aphids) of remnant habitats are not like their desert counterparts even though habitat structure (plants) is similar. The timing of peak growth and abundances (phenology) was sometimes more similar to urban habitats than desert habitats. This has important implications for biodiversity conservation in cities, as it suggests that simply preserving habitats is not enough to maintain original community structure and natural fluctuations (Palmer et al. 1997, Faeth et al. 2011).

Trophic dynamics in cities

Caution is advised when extrapolating our results to non-arid cities. Water is an important factor in arid and desert ecosystems, and an increase in water stimulates productivity. In other cities, water may not be limiting for productivity. Urban ecosystems in arid areas have, in addition to water, local features that contribute to high productivity, such as sheltering buildings and the urban heat island (Kuttler 2008). These features are shared with many cities around the world, even if water is not limiting. Another effect of urbanization is an increase in nitrogen deposition and CO₂ uptake, which can be significant for plant growth (Gregg et al. 2003, Grimm et al. 2008a, Trusilova and Churkina 2008). It is therefore reasonable to expect increased productivity in most cities in comparable habitat types relative to wildland habitats, which then provides a template for bottom-up forces (Faeth et al. 2011).

Understanding the factors that determine biodiversity and trophic structure are two of the central pursuits of ecology. There is ample evidence that both resources and consumers determine species richness and trophic structure (Paine 1966, Rosenzweig 1973, Oksanen and Oksanen 2000, Price and Hunter 2005, Redfern and Hunter 2005). Most of this evidence comes from ecosystems that are outside of urban cores. Here, we have presented some of the first experimental evidence that the controls of biodiversity and trophic dynamics are qualitatively different in urban settings. The effect of

urban development in many cases overrides the effects of more traditional mechanisms leading to community structure (resources and consumers).

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LITERATURE CITED

- Baker, L. A., A. J. Brazel, N. Selover, C. Martin, N. McIntyre, F. R. Steiner, A. Nelson, and L. Musacchio. 2002. Urbanization and warming of Phoenix (Arizona, USA): Impacts, feedbacks and mitigation. *Urban Ecosystems* 6:183–203.
- Bale, J. S., R. Harrington, and M. S. Clough. 1988. Low temperature mortality of the peach-potato aphid *Myzus persicae*. *Ecological Entomology* 13:121–129.
- Bang, C., J. L. Sabo, and S. H. Faeth. 2010. Reduced wind speed improves plant growth in a desert city. *PLoS ONE* 5:e11061.
- Bartlett, T. 2005. Bugguide.net [hosted by Iowa State University]. <http://bugguide.net/search/>
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: individuals, populations, and communities*. Third edition. Blackwell Science, Oxford, UK.
- Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society* 9(2):5.
- Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. *An introduction to the study of insects*. Sixth edition. Saunders College Publishing, Philadelphia, Pennsylvania, USA.
- Cadenasso, M. L., S. T. A. Pickett, and K. Schwarz. 2007. Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. *Frontiers in Ecology and the Environment* 5:80–88.
- Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74:46–69.
- Chapin, F. S., III, P. A. Matson, and H. A. Mooney. 2002. *Principles of terrestrial ecosystem ecology*. Springer-Verlag, New York, New York, USA.
- Chapin, F. S., III, B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277:500–504.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Collinge, S. K. 1996. Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. *Landscape and Urban Planning* 36:59–77.
- Colwell, R. K. 2006. EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Persistent URL purl.oclc.org/estimates
- Comstock, J., and J. Ehleringer. 1986. Canopy dynamics and carbon gain in response to soil-water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia* 68:271–278.
- Cordero, R. A., N. Fetcher, and J. Voltzow. 2007. Effects of wind on the allometry of two species of plants in an elfin cloud forest. *Biotropica* 39:177–185.
- Crawford, C. S. 1986. The role of invertebrates in desert ecosystems. Pages 73–92 in W. G. Whitford, editor. *Pattern*

- and process in desert ecosystems. University of New Mexico Press, Albuquerque, New Mexico, USA.
- Ehleringer, J. R. 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *American Journal of Botany* 69:670–675.
- Ehleringer, J. R., and C. S. Cook. 1984. Photosynthesis in *Encelia farinosa* Gray in response to decreasing leaf water potential. *Plant Physiology* 75:688–693.
- Ehleringer, J. R., and C. S. Cook. 1990. Characteristics of *Encelia* species differing in leaf reflectance and transpiration rate under common garden conditions. *Oecologia* 36:151–162.
- Faeth, S. H., C. Bang, and S. Saari. 2011. Urban biodiversity: patterns and mechanisms. *Annals of the New York Academy of Sciences* 1223:69–81.
- Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. *BioScience* 55:399–407.
- Floyd, T. 1996. Top-down impacts on creosotebush herbivores in a spatially and temporally complex environment. *Ecology* 77:1544–1555.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81:1588–1600.
- Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50:291–301.
- Gober, P., and E. K. Burns. 2002. The size and shape of Phoenix's urban fringe. *Journal of Planning Education and Research* 21:379–390.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Gotelli, N. J., and G. L. Entsminger. 2009. EcoSim: null models software for ecology. Version 7.72. Acquired Intelligence, Inc., and Kesey-Bear, Jericho, Vermont, USA.
- Grigg, J. W., C. G. Jones, and T. E. Dawson. 2003. Urbanization effects on tree growth in the vicinity of New York City. *Nature* 424:183–187.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. G. Wu, X. M. Bai, and J. M. Briggs. 2008a. Global change and the ecology of cities. *Science* 319:756–760.
- Grimm, N. B., D. Foster, P. Groffman, J. M. Grove, C. S. Hopkinson, K. J. Nadelhoffer, D. E. Pataki, and D. P. C. Peters. 2008b. The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment* 6:264–272.
- Gruner, D. S., and A. D. Taylor. 2006. Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. *Oecologia* 147:714–724.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142:379–411.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1–9.
- Hazell, S. P., C. Groutides, B. P. Neve, T. M. Blackburn, and J. S. Bale. 2010. A comparison of low temperature tolerance traits between closely related aphids from the tropics, temperate zone, and Arctic. *Journal of Insect Physiology* 56:115–122.
- Holmes, R. T., J. C. Schultz, and P. Nothnagle. 1979. Bird predation on forest insects: an enclosure experiment. *Science* 206:462–463.
- Hope, D., C. Gries, W. Zhu, W. F. Fagan, C. L. Redman, N. B. Grimm, A. L. Nelson, C. Martin, and A. Kinzig. 2003. Socioeconomics drive urban plant diversity. *Proceedings of the National Academy of Sciences USA* 100:8788–8792.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Hunter, M. D., and J. C. Schultz. 1993. Induced plant defenses breached? Phytochemical induction protects an herbivore from disease. *Oecologia* 94:195–203.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586.
- Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University Of Chicago Press, Chicago, Illinois, USA.
- Koehler, C. E. 2003. *Encelia farinosa* Gray ex Torr. brittlebush. <http://www.fs.fed.us/global/iitf/pdf/shrubs/Encelia%20farinosa.pdf>
- Kühn, I., R. Brandl, and S. Klotz. 2004. The flora of German cities is naturally species rich. *Evolutionary Ecology Research* 6:749–764.
- Kunze, A., C. Muller, and P. Proksch. 1995. Chemical variation and defense of *Encelia farinosa*. *Biochemical Systematics and Ecology* 23:355–363.
- Kuttler, W. 2008. The urban climate – basic and applied aspects. Pages 233–248 in J. M. Marzluff, E. Schulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, C. ZumBrunnen, and U. Simon, editors. *Urban ecology - an international perspective on the interaction between humans and nature*. Springer Verlag, New York, New York, USA.
- Lambers, H., F. S. Chapin III and T. L. Pons. 1998. *Plant physiological ecology*. Springer-Verlag, New York, New York, USA.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922–949.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–418.
- Lyon, D. L., J. Crandall, and M. McKone. 1977. A test of the adaptiveness of interspecific territoriality in the Blue-throated Hummingbird. *Auk* 94:448–454.
- Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007–2014.
- Martin, C. A., and L. B. Stabler. 2002. Plant gas exchange and water status in urban desert landscapes. *Journal of Arid Environments* 51:235–254.
- Martin, C. A., P. S. Warren, and A. P. Kinzig. 2004. Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in residential neighborhoods and embedded small parks of Phoenix, Arizona. *Landscape and Urban Planning* 69:355–368.
- Marussich, W. A., and S. H. Faeth. 2009. Effects of urbanization on trophic dynamics of arthropod communities on a common desert host plant. *Urban Ecosystems* 12:265–286.
- Marzluff, J. M., R. Bowman, and R. Donnelly, editors. 2001. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Boston, Massachusetts, USA.
- McGranahan, G., P. Marcotullio, X. Bai, D. Balk, T. Braga, I. Douglas, T. Elmquist, W. Rees, D. Satterthwaite, J. Songso, and H. Zlotnik. 2005. *Urban systems*. Pages 795–825 in R. Hassan, S. Scholes, and N. Ash, editors. *Millennium ecosystem assessment, current state and trends: Findings of the condition and trends working group*. Ecosystems and human well-being. Island Press, Washington, D.C., USA.
- McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. *Annals of the Entomological Society of America* 93:825–835.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. *BioScience* 52:883–890.
- Menge, B. A., and J. P. Sutherland. 1976. Species-diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110:351–369.

- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730–757.
- Murdoch, W. W. 1966. “Community structure, population control, and competition”—a critique. *American Naturalist* 100:219–226.
- Neil, K. 2008. Effects of urbanization on flowering phenology in Phoenix, USA. Dissertation. Arizona State University, Tempe, Arizona, USA.
- Nobel, P. S., H. H. Zhang, R. Sharifi, M. Castaneda, and B. Greenhouse. 1998. Leaf expansion, net CO₂ uptake, Rubisco activity, and efficiency of long-term biomass gain for the common desert subshrub *Encelia farinosa*. *Photosynthesis Research* 56:67–73.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–51.
- Noy-Meir, I. 1974. Desert ecosystems: Higher trophic levels. *Annual Review of Ecology and Systematics* 5:195–214.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240–261.
- Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* 155:703–723.
- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* 104:377–387.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291–300.
- Pinheiro, M. H. O., L. Neto, and R. Monteiro. 2006. Urban areas and isolated remnants of natural habitats: an action proposal for botanical gardens. *Biodiversity and Conservation* 15:2747–2764.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73:733–746.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11:41–65.
- Price, P. W., and M. D. Hunter. 2005. Long-term population dynamics of a sawfly show strong bottom-up effects. *Journal of Animal Ecology* 74:917–925.
- Redfern, M., and M. D. Hunter. 2005. Time tells: long-term patterns in the population dynamics of the yew gall midge, *Taxomyia taxi* (Cecidomyiidae), over 35 years. *Ecological Entomology* 30:86–95.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* 107:275–294.
- Sandquist, D. R., and J. R. Ehleringer. 2003. Population- and family-level variation of brittlebush (*Encelia farinosa*, Asteraceae) pubescence: Its relation to drought and implications for selection in variable environments. *American Journal of Botany* 90:1481–1486.
- SAS Institute. 2008. SAS version 9.92 for Windows. SAS Institute, Cary, North Carolina, USA.
- Schmitz, O. J., and L. Sokol-Hessner. 2002. Linearity in the aggregate effects of multiple predators in a food web. *Ecology Letters* 5:168–172.
- Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* 60:199–208.
- Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *American Naturalist* 164:232–243.
- Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* 21:186–191.
- Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. *Ecology* 75:182–196.
- Stiles, F. G. 1971. Time, energy, and territoriality of the Anna Hummingbird (*Calypte anna*). *Science* 173:818–821.
- Stiling, P., and A. M. Rossi. 1996. Complex effects of genotype and environment on insect herbivores and their enemies. *Ecology* 77:2212–2218.
- Stiling, P., and A. M. Rossi. 1997. Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology* 78:1602–1606.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754.
- Tesky, J. L. 1993. *Encelia farinosa*. Fire effects information system. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Fort Collins, Colorado, USA. <http://www.fs.fed.us/database/feis/>
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.
- Trusilova, K., and G. Churkina. 2008. The response of the terrestrial biosphere to urbanization: land cover conversion, climate, and urban pollution. *Biogeosciences* 5:1505–1515.
- Walker, J. S., N. B. Grimm, J. M. Briggs, C. Gries, and L. Dugan. 2009. Effects of urbanization on plant species diversity in central Arizona. *Frontiers in Ecology and the Environment* 7:465–470.
- White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* 33:71–86.

SUPPLEMENTAL MATERIAL

Appendix

Experimental setup, winter temperature data, full ANOVA tables, and a list of identified arthropods and their feeding guilds (*Ecological Archives*: M082-003-A1).

Data Availability

Data associated with this paper are publicly available through the Central Arizona-Phoenix (CAP) LTER website: <http://caplter.asu.edu/data/>