

Ground arthropod community structure in a heterogeneous urban environment

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Abstract

Despite being conspicuous and influential features of the biosphere, urban ecosystems have been neglected in ecological research. Arthropods are abundant in urban settings, but little is known about how these animals respond to urbanization. We systematically monitored the structure of ground arthropod communities for 12 months at 16 sites representing the four most abundant forms of urban land use (residential, industrial, agricultural, and desert remnant) in a rapidly growing metropolitan area (Phoenix, AZ). Although taxonomic richness was comparable among land-use types, community composition differed, with certain taxa being uniquely associated with each form of land use. Three taxa (springtails, ants, and mites) were extremely widespread and abundant, accounting for over 92% of captures; when these three taxa were excluded from analysis, however, differences were revealed in arthropod community composition with urban land use. Trophic dynamics also varied with land use: predators, herbivores, and detritivores were most abundant in agricultural sites, while omnivores were equally abundant in all forms of land use. These community-level differences resulted from taxon-specific responses to habitat structure, which varied with land use. Because arthropod community structure is affected by habitat structure and land use, and because arthropods play key roles in nutrient cycling, organic matter decomposition, pollination, and soil aeration, the spatial heterogeneity of urban ecosystems therefore may affect ecosystem functioning. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Half of the world's human population currently lives in urban areas (defined here as any area with a human population density >620 individuals/km²; US Census Bureau, 1980); this figure is predicted to increase to 66% over the next 25 years (World Bank, 1984; United Nations Population Division, 1995).

Urban ecosystems are generally recognized as areas under profound and constant local human activity, being composed of high-density human habitation, industrial and commercial centers, and remnants of indigenous habitat. Urbanization is the process whereby urban ecosystems are created. This process entails conversion of indigenous habitat to various forms of anthropogenic land use, fragmentation and isolation of areas of indigenous habitat, and an increase in local human population density. Urban ecosystems are thus characterized as spatially heterogeneous and temporally dynamic areas that differ

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from their current surroundings and from previous conditions with respect to greater presence of impervious surfaces (e.g., through soil compaction and paving), pollution (light, noise, atmospheric, and aquatic), higher numbers of exotic species (particularly plants; Rebele, 1994), and changes to local climate (e.g., through the urban “heat island” effect; Kim, 1992) (Vitousek et al., 1997). The primary distinguishing feature of urban ecosystems, however, is that the amount of energy consumed per unit area is at least one order of magnitude greater than in other types of ecosystems (including other human-dominated ecosystems, such as agroecosystems; Odum, 1997). For example, coastal estuaries are extremely diverse, dynamic ecosystems whose inhabitants collectively consume approximately 70 kcal/m²/day. Urban systems (considered collectively around the globe) are estimated to consume over 55 times that amount. Thus, even though urban areas cover a relatively small percentage of the Earth’s surface (<5%), they consume the vast majority of the energy available to the Earth (Odum, 1997). All of these characteristics may have far-reaching effects on regional biota. Until recently, many people perceived urban areas to be replacements of “natural” habitat and therefore devoid of ecological interest. Recently, however, it has become apparent that urban areas may be considered ecosystems in their own right, with feedback loops among both “natural” and anthropogenic forms of the physical and biological setting (McDonnell and Pickett, 1993; Botkin and Beveridge, 1997; Rees, 1997; Vitousek et al., 1997; Walbridge, 1997; Parlange, 1998). As a consequence, biologists are now beginning to assess the effects of urbanization on biotic communities. Since urban development is expected to increase in both scope and magnitude, knowledge about how the urban ecosystem functions will be useful in planning future urban development that will minimize environmental impacts.

Despite their global ubiquity, surprisingly little is known about how arthropods respond to urbanization (McIntyre, 2000), even though urbanization has been identified as one of the leading causes of declines in arthropod diversity and abundance (Davis, 1978; Pyle et al., 1981). Although there have been some studies of specific taxa (primarily pest species) in urban settings (Ebeling, 1978; Frankie and Ehler, 1978; Dreistadt et al., 1990), these studies were primarily concerned

with focal insect species rather than entire arthropod assemblages. Examining arthropod community structure as a whole may provide more general insights into the phenomenon of urbanization (Zapparoli, 1997; McIntyre, 2000).

Arthropods are excellent candidates for studying how the formation of urban ecosystems impacts the environment for a number of reasons. Foremost of these is the variety of roles played by arthropods in ecosystem functioning (e.g., food web dynamics, nutrient cycling and redistribution, and pollination), with many of these roles being economically important (e.g., pollination by domestic bees is \$18 billion/year industry in the US alone; Levin, 1983). Arthropods are abundant, enabling large sample sizes to be obtained for high statistical power. Arthropods are also relatively easy to sample compared to larger and less abundant animals (e.g., vertebrates). Most arthropods have relatively short generation times, meaning that arthropod populations have the capacity to respond quickly to the rapid pace of urbanization. Finally, because habitat changes wrought by urbanization are considered among the leading causes of declines in arthropod diversity and abundance around the world, the conservation of arthropods threatened by urban development is a timely and pressing issue (Pyle et al., 1981; Clark and Samways, 1997).

Urbanization may have a variety of effects on the local arthropod assemblages, based upon conversion of indigenous habitat to anthropogenic habitat. If arthropods respond to habitat structure, then we predict that there will be differences in species assemblages among different forms of urban land use (residential, industrial, agricultural, and remnant desert), which differ in habitat structure. Communities in residential, industrial, and agricultural land are predicted to be subsets of desert (indigenous) communities. Furthermore, we predict agricultural land to be the most different from remnant desert since no native vegetation is used in agricultural land, unlike in residential and industrial sites. We test these predictions in this paper. Our objectives are: (1) to describe the composition and turnover of the ground arthropod community of the Phoenix, AZ, metropolitan area with respect to the four most abundant types of urban land use; (2) to determine which taxa are indicative of those forms of urban land use; (3) to explore how correlations between habitat structure and urban land

use may account for variation in ground arthropod community structure; (4) to compare the community composition and functional roles of arthropods in different types of urban land use. Our study highlights how various facets of urbanization affect the diversity and distribution of ground arthropods, which may have important ramifications on ecosystem-level trophic dynamics, nutrient cycling, and other functions that ground arthropods perform in ecosystems. Identification of taxa that appear to be particularly indicative of different forms of urban land use may expedite detection of latent forms of urbanization and facilitate future studies. In characterizing ground arthropod assemblages as functions of land use in a large and expanding metropolitan area, we may better predict (and thereby preserve) patterns of arthropod diversity and ecosystem responses to future urban development. Because urban ecology is such a new field, our results should lay the groundwork for future studies in urban ecosystems.

2. Methods

2.1. Study sites

The Sonoran Desert is a 275 000 km² biome that is characterized by mild to extremely hot temperatures and two seasonal periods of rain (the winter/spring rainy period from December to March and the summer “monsoon” from July to September) (MacMahon and Wagner, 1985). The Sonoran Desert possesses a diverse arthropod fauna, including numerous taxa that are found in no other biome (MacMahon and Wagner, 1985). A portion of this biome is currently being converted into the desert metropolis of Phoenix, AZ.

The Phoenix metropolitan area covers approximately 3900 km² (AZB, 1998). With a human population of $\sim 2.7 \times 10^6$ and an annual population growth rate exceeding 22%, this area is expanding rapidly. Indeed, Phoenix is the second-fastest-growing metropolitan area in US, located within the fastest-growing county in the nation (AZB, 1998; Gober, 1998). There are 24 incorporated cities in the Phoenix metropolitan area, collectively comprising a heterogeneous mosaic of residential lots, retail properties, industrial complexes, agricultural fields, and other forms of anthropogenic land use, along with remnant areas of

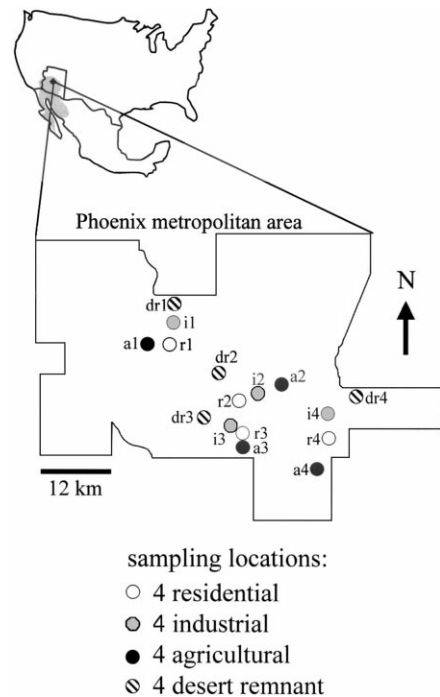


Fig. 1. Location of the 16 arthropod sampling locations in the Phoenix metropolitan area (black diamond), Arizona, located within the Sonoran Desert (gray area). Boundaries of the Sonoran Desert follow MacMahon and Wagner (1985). Site names correspond to those in Table 1, with a: agricultural, r: residential, dr: desert remnant, i: industrial.

indigenous Sonoran Desert habitat. This rapidly growing mosaic structure makes Phoenix ideal in examining how urbanization affects arthropod community composition, for it allows simultaneous comparisons to be made across a spatially heterogeneous region.

We surveyed ground arthropods at 16 sites throughout the Phoenix metropolitan area (Fig. 1). These sites were chosen to represent a wide geographic coverage of Phoenix (following a NW to SE trajectory, corresponding to major access roads). Sites were separated by an average of 26 km (linear distance; range: 2.5–59 km). The sites represented the four most abundant forms of urban land use in the Phoenix metropolitan area (residential, industrial, agricultural, and desert remnant), with four replicate sites per type of land use (Table 1). These four categories comprise 97.2% of the total amount of land use in the Phoenix metropolitan area (Fig. 2) (MAG, 1998). *Residential* sites were defined by presence of single-family homes with

Table 1
Descriptions of the 16 study sites

Site name ^a	Site location	UTM coordinates ^b
Agricultural 1	NW 83rd Ave., Thunderbird Rd. cotton, Peoria	3719513, 385212
Agricultural 2	SE Dobson Rd., Hwy. 202 alfalfa, Mesa	3699613, 419318
Agricultural 3	SE 56th Ave., Chandler Blvd. alfalfa, Chandler	3685074, 410517
Agricultural 4	SW Power Rd., Elliot Rd. alfalfa, Gilbert	3690110, 435977
Residential 1	W. Hearn Rd., Phoenix	3719820, 396019
Residential 2	W. 19th St., Tempe	3696788, 412223
Residential 3	Jeanine St., Tempe	3687847, 410783
Residential 4	Douglas Ave., Higley	3691798, 435991
Desert remnant 1	Adobe Dam Recreation Area, Phoenix	3727724, 394768
Desert remnant 2	Desert Botanical Garden, Phoenix	3702692, 412390
Desert remnant 3	South Mountain Regional Park, Phoenix	3691377, 406630
Desert remnant 4	Usery Mountain Park, Mesa	3703508, 442938
Industrial 1	Honeywell IAC, Union Hills Dr., Phoenix	3724675, 396993
Industrial 2	Arizona Public Service Ocotillo Plant, Tempe	3698717, 414987
Industrial 3	Insight, S. Harl Ave., Tempe	3691068, 410007
Industrial 4	Valley Lutheran Hospital, Baywood Ave., Mesa	3696900, 436088

^a Note that “site name” also denotes land-use type.

^b UTM coordinates (NAD, 1927, zone 12) are northing, easting coordinates expressed in meters.

xeriscaped yards (i.e., non-turf, being instead comprised of gravel), *industrial* by presence of non-residential commercial structures (e.g., warehouses) and xeric landscaping, *agricultural* by presence of tilled row crops (alfalfa (*Medicago sativa*) or cotton (*Gossypium hirsutum*)), and *desert remnant* by lack of built structures and presence of Sonoran Desert vegetation (e.g., saguaro (*Carnegiea gigantea*), cholla (*Opuntia*

spp.), ironwood (*Olneya tesota*), mesquite (*Prosopis* spp.), creosote bush (*Larrea tridentata*), and/or palo verde (*Cercidium* spp.)).

Categorizing sites by land-use type, a common practice in urban ecology (e.g., Czechowski and Mikolajczyk, 1981; Czechowski, 1982; Blair, 1996; Blair and Launer, 1997), tends to ignore site-specific differences in physical habitat structure. Sites belonging to the same land-use type may in fact not be true replicates of one another with respect to resources for arthropods, resulting in differences in the ground arthropod community among “replicate” areas. Site-specific features make true replication of landscapes difficult. Therefore, it is important to quantify site characteristics to determine to what degree a site is truly representative of a broader category such as a type of land use. We did so by measuring a variety of habitat parameters at each site, which were then used to distinguish physical features characteristic of each of the four types of land use. Habitat characteristics were measured in early 1999 (February–April), a period of new growth when plants can be most readily identified before summer senescence. The percent horizontal ground cover of native trees, native shrubs, exotic trees, exotic shrubs, cacti, grass, herbaceous annual plants, soil, rocks, grass (lawn), gravel,

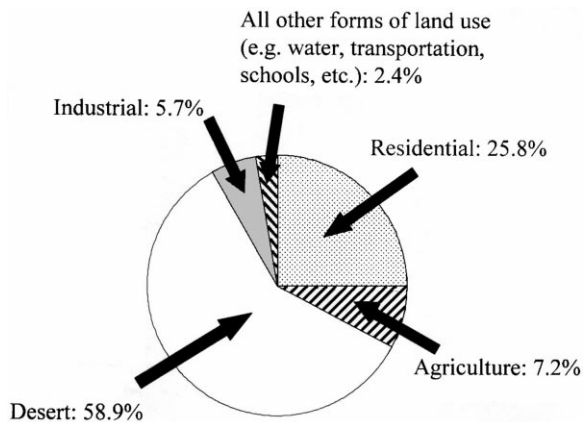


Fig. 2. Pie diagram showing the proportion of different forms of land use in the Phoenix metropolitan area (data from MAG, 1998).

Table 2
Percent horizontal cover of habitat features at each of the 16 study sites

Habitat feature	Percent horizontal ground cover present in site															
	Agriculture				Residential				Desert				Industrial			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Native trees	0	0	0	0	3	0	0	1	5	1	10	1	5	1	0	1
Exotic trees	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0
Native shrubs	0	0	0	0	0	0	0	1	25	40	10	10	0	0	25	1
Exotic shrubs	0	0	0	0	0	1	0	1	0	0	0	0	3	0	0	0
Cactus	0	0	0	0	5	0	1	5	1	0	10	0	2	0	0	1
Herbaceous	0	0	0	0	2	3	0	20	0	5	5	0	0	5	10	47
Bare soil	0	0	0	0	20	15	23	0	69	44	65	45	65	85	55	20
Rock	0	0	0	0	0	0	0	0	0	10	0	44	0	1	0	0
Grass (lawn)	0	0	0	0	5	10	55	5	0	0	0	0	0	3	10	10
Gravel	0	0	0	0	25	10	0	20	0	0	0	0	0	0	0	10
Concrete	0	0	0	0	1	30	10	10	0	0	0	0	25	5	0	10
Buildings	0	0	0	0	35	30	10	36	0	0	0	0	0	0	0	0
Swimming pools	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Other (crop)	100	100	100	100	0	0	0	0	0	0	0	0	0	0	0	0

concrete, buildings, and swimming pools were measured within a 25-m-diameter circle centered around the midpoint of a site's trap transect (see *ground arthropod sampling*, below) (Table 2). Percent horizontal ground cover was estimated by eye by an observer standing at the circle's center. All measurements were performed by one person (NEM) to avoid multi-observer bias in measurements. Plant species names and categorizations are given in Table 3. Percent horizontal ground cover values were arcsine-transformed for statistical analyses (Sokal and Rohlf, 1981). Values were averaged among the four replicate sites within each type of land use.

These characteristics were used to determine to what degree our study sites resembled one another in terms of structure and composition. Cluster analysis (using the average linkage method; SAS, 1996) was used to determine the degree of similarity among our 16 study sites, particularly to determine whether sites that were geographically close to one another were also similar in terms of arthropods present, regardless of differences in land-use type. Discriminant function analysis (DFA) was used to determine how well our four a priori land-use classifications (residential, industrial, agricultural, and desert remnant) differentiated our sites in terms of the habitat features present (Johnson and Wichern, 1992). Good predictive

capacity indicated from the overall DFA (i.e., error rate <50%) was followed by Tukey's Studentized Range multiple comparisons on the individual variables to quantify differences and similarities among land-use types (SAS, 1996).

2.2. Ground arthropod sampling

We collected arthropods using 10 dry, unbaited pitfall traps at each of our 16 sites. Despite concerns about various biases inherent to certain trap designs (Southwood, 1966; Luff, 1975; Adis, 1979; Spence and Niemela, 1994), pitfall trapping remains the most appropriate means of sampling a diverse suite of ground arthropods (Ausden, 1996). Traps were spaced 5 m apart along a line transect (straight line at industrial, agricultural, and desert-remnant sites; straight line constrained by property boundaries at residential sites). Traps were placed in flat areas, perpendicular to slopes. Traps consisted of two 500 ml plastic cups, with one cup stacked inside the other. The lip of the inner cup was set flush to the ground surface, and the lip of the outer cup was set slightly below the surface. The outer cup remained in the ground, whereas the inner cup and its contents could be removed easily without displacing the entire trap. Traps were set for 72 consecutive hours once each month for 12 months

Table 3
Species name and categorization of plants recorded at the 16 study sites

Common name	Species name	Categorization ^a
Desert (sweet) acacia	<i>Acacia smallii</i>	Native tree
Blue palo verde	<i>Cercidum floridum</i>	Native tree
Foothills palo verde	<i>Cercidum microphyllum</i>	Native tree
Ironwood	<i>O. tesota</i>	Native tree
Cottonwood	<i>Populus</i> sp.	Native tree
Mesquite	<i>Prosopis</i> sp.	Native tree
Desert fan palm	<i>Washingtonia filifera</i>	Native tree
Citrus	<i>Citrus</i> sp.	Exotic tree
Grapefruit	<i>Citrus × paradisi</i>	Exotic tree
Australian willow	<i>Geijera parviflora</i>	Exotic tree
Pine	<i>Pinus</i> sp.	Exotic tree
Peach	<i>Prunus persica</i>	Exotic tree
African sumac	<i>R. lancea</i>	Exotic tree
Chinese elm	<i>Ulmus parvifolia</i>	Exotic tree
Pepper tree	<i>Vitex agnis</i>	Exotic tree
Saguaro	<i>C. gigantea</i>	Cactus
Night-blooming cereus	<i>Cereus schottii</i> f. <i>monstruosus</i>	Cactus
Strawberry hedgehog cactus	<i>Echinocereus engelmannii</i>	Cactus
Golden barrel cactus	<i>Echinocactus grusonii</i>	Cactus
Barrel cactus	<i>Ferocactus wislizenii</i>	Cactus
Prickly pear cactus	<i>Opuntia</i> spp.	Cactus
Buckhorn cholla	<i>Opuntia acanthocarpa</i>	Cactus
Teddy bear cholla	<i>Opuntia bigelovii</i>	Cactus
Chain fruit cholla	<i>Opuntia fulgida</i>	Cactus
Century plant	<i>Agave</i> spp.	Native shrub
Bursage	<i>Ambrosia</i> spp.	Native shrub
Four-wing saltbush	<i>Atriplex canescens</i>	Native shrub
Desert broom	<i>Baccharis sarathroides</i>	Native shrub
Ocotillo	<i>Fouquieria splendens</i>	Native shrub
Creosote bush	<i>L. tridentata</i>	Native shrub
Texas ranger	<i>Leucophyllum frutescens</i>	Native shrub
Yucca	<i>Yucca</i> spp.	Native shrub
Bougainvillea	<i>Bougainvillea spectabilis</i>	Exotic shrub
Fire thorn	<i>Pyreacantha</i> sp.	Exotic shrub
Rose	<i>Rosa cathayensis</i>	Exotic shrub
Desert petunia	<i>Ruellia peninsularis</i>	Exotic shrub
Tumbleweed	<i>Salsola</i> spp.	Exotic shrub

^a Categorization follows Ellis (1989) and Epple (1995).

(June 1998–May 1999). Trap contents were collected and preserved in 70% ethyl alcohol. Traps were closed with tight-fitting plastic lids when not in use.

Adult insects and spiders were identified to Family; other adult arthropods were identified to Order (following Borror et al. (1989)). Juvenile arthropods and members of taxa whose primary means of locomotion is flight (i.e., Diptera, Lepidoptera, Odonata, Neuroptera, and Hymenoptera excluding Formicidae and Mutillidae) were excluded from analysis because

pitfall trapping is inappropriate for sampling these groups (Ausden, 1996). Voucher specimens are housed in the Department of Biology at Arizona State University, Tempe, AZ.

The taxonomy of most Sonoran Desert arthropods is very poorly known, but identification to Order and Family can be made with confidence. Conducting identifications to broad levels is an efficient way of assessing biodiversity rapidly and is therefore likely to be used by land-use planners and urban environmental

consultants who are concerned with rapid turnover in biota resulting from urban change. Since arthropods are important components of ecosystems, it is imperative that there be streamlined alternatives for planners and consultants to use instead of ignoring arthropods altogether because of their taxonomic complexity.

Ground arthropod community structure (taxonomic richness, abundance, community similarity, and community composition) was assessed at each site in each month over the entire study period. These values were compared across months, seasons (spring, summer, autumn, and winter), and the four land-use types (industrial, agricultural, residential, and desert remnant). Arthropod taxa were also classified according to trophic position (predator, herbivore, detritivore, or omnivore) and compared by site, land-use type, month, and season. Differences in the proportion of various trophic levels among site types may indicate differences in ecosystem functions with urban land use. Although a Family or Order may contain multiple trophic positions, taxa were assigned to trophic level according to whether the majority of members of the taxon were carnivorous, phytophagous, detritivorous, or omnivorous (following dietary information in Borror et al. (1989)). Some taxa (e.g., some Coleoptera families) could not be readily assigned to only one of these groups and were therefore excluded from trophic analysis.

Repeated-measures multivariate analysis of variance (MANOVA) was used to compare average arthropod richness and number of individuals captured among sites, land-use types, months, and seasons. Significant MANOVA models were followed by univariate analysis of variance (ANOVA) and Tukey's Studentized Range tests to compare richness and abundance among class variables (site, land-use type, month, and season). Morisita's index (MI) of community similarity (a pairwise index based on species' abundances rather than simple presence/absence; Morisita, 1959) was calculated to compare community composition by site and land-use type. The index ranges from 0 (denoting no similarity in community composition between sites) to 1 (denoting complete overlap) (Krebs, 1989). High values of MI indicate that there are similar patterns of dominance among taxa between the two sites being compared (i.e., taxa that are abundant at one site are likewise abundant at the other site, and taxa that are rare at one site are

likewise rare at the other site). This index is considered to be one of the most robust measures of community similarity (Wolda, 1981). MI was calculated for each of six pairwise comparisons between the four land-use types (e.g., desert vs. agricultural, desert vs. residential, etc.) as well as for each of six pairwise comparisons between the four replicate members of each land-use type (e.g., desert site 1 vs. desert site 2, etc.). An average was then calculated over the replicate index values.

Because arthropods are ectotherms, their activity is dictated by climatic conditions. To determine how this relationship is mediated by urban land use, daily air temperatures and precipitation levels were acquired from the National Oceanic and Atmospheric Administration (NOAA) weather station at Sky Harbor Airport in Phoenix. Spearman correlations were used to determine whether taxonomic richness, abundance, and the two climate variables were correlated in the four land-use types.

Canonical correspondence analysis (CCA) was used to relate arthropod community composition to site habitat variables. CCA is a community ordination technique that relates community composition to quantitative or categorical environmental variables, such as percent ground cover, temperature, or soil type (ter Braak, 1986; ter Braak and Prentice, 1988). CCA visualizes this relationship by using multiple linear least-squares regression to generate axes that are linear combinations of environmental variables; taxa abundances are then plotted within the axes' ordination space (Palmer, 1993). Monte Carlo randomization tests (using 99 simulations) were used to determine the significance of the axes (Blair, 1996; Blair and Launer, 1997; French and Elliott, 1999). CCA is a robust multivariate form of gradient analysis that has great potential for examining how organisms respond to changes in habitat structure along gradients of urban development. For example, CCA has been successfully used to analyze how community composition varies according to shifts in habitat structure along urban–rural gradients for butterflies (Blair and Launer, 1997) and birds (Blair, 1996; Rottenborn, 1999). It has also been used to determine how the abundances of various carabid beetle species vary with season and habitat type (French and Elliott, 1999). CCA performs well using abundance data from pitfall traps (Palmer, 1993; French and Elliott, 1999). CCA

and Monte Carlo simulations were performed using PC-ORD 3.2 (McCune and Mefford, 1997); all other statistical analyses were performed using SAS[®] 6.12 (SAS, 1996).

3. Results

A total of 175 000 ground arthropods belonging to 73 taxa were captured (Appendix A). Repeated-measures MANOVA revealed that there were significant differences among the variables we measured (Wilks' lambda: $F_{11} = 21.02$, $P = 0.0001$): taxonomic richness differed among the 16 sites (ANOVA: $F_{15} = 6.25$, $P = 0.0001$), the four land-use types ($F_3 = 9.31$, $P = 0.0001$), months ($F_{11} = 16.08$, $P = 0.0001$), and seasons ($F_3 = 8.43$, $P = 0.0074$).

Of the 73 taxa collected, 26 were represented by <10 individuals, and four of these taxa were represented by only a single individual. Springtails (Collembola), ants (Hymenoptera: Formicidae), and mites (Acari) were by far the most abundant taxa sampled, collectively accounting for 92.7% of the total number of individuals captured (Collembola: 65.7%, Formicidae: 15.0%, Acari: 12.0%). Members of these three

taxa occurred at all 16 sites, in all 4 land-use types, in all months and seasons, although they were not completely ubiquitous (i.e., there were some months where one or more of these taxa were not captured in at least one site). Including springtails, mites, and ants, 41 taxa were found in all four land-use types. The next most abundant taxa were (in order of abundance): Coleoptera: Tenebrionidae (0.75% of total individuals), Dermaptera: Labiduridae (0.71%), Coleoptera: Carabidae (0.68%), Hemiptera: Lygaeidae (0.61%), Araneae: Lycosidae (0.50%), Blattaria: Blattidae (0.47%), and Hemiptera: Aphididae (0.46%). All remaining taxa accounted for $\leq 0.01\%$ of total captures.

Contrary to our initial predictions, the taxa in residential, industrial, and agricultural forms of land use were not perfect subsets of the taxa found in desert remnants; rather, all four forms of land use contained both shared and unique taxa. Desert-remnant sites possessed seven unique taxa (i.e., taxa not found in the other land-use types, denoted in Appendix A), followed by agricultural (two unique taxa), residential (2), and industrial (2) sites. Despite these differences in richness, the number of individuals captured did not differ with land-use type ($F_3 = 0.91$, $P = 0.4631$) (Fig. 3).

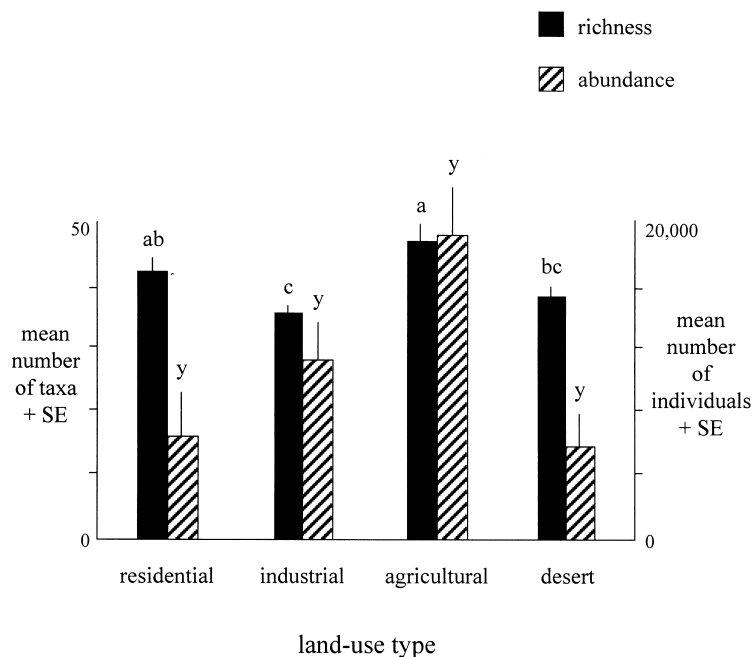


Fig. 3. Mean (+S.E.) taxonomic richness (left-hand Y-axis) and number of individuals (right-hand Y-axis) by land-use type.

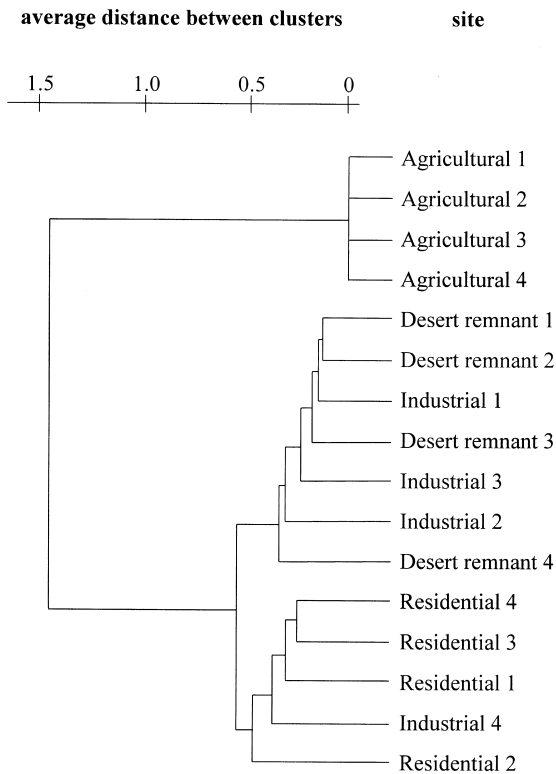


Fig. 4. Dendrogram depicting results of cluster analysis for similarity in habitat features (see Tables 2 and 3) among our 16 study sites.

The four land-use designations we used (residential, industrial, agricultural, and desert remnant) were fairly accurate in representation of structural and compositional habitat differences among our 16 study sites. DFA revealed that our sites could be classified to their appropriate land-use type the majority of the time (error rate = 35.94%), although there was some variation among sites within a land-use type. For example, one of our agricultural sites was planted with cotton, whereas the other three sites had alfalfa. Additionally, one of our residential sites possessed a large African sumac tree (*Rhus lancea*) with a spreading canopy, whereas the other three yards were relatively unshaded. Cluster analysis indicated that three of the four industrial sites were more similar to the desert remnants in terms of habitat features, whereas the fourth industrial site resembled the residential yards (Fig. 4). This industrial site, the cotton field, and the shaded residential site accounted for most of the misclassification error in our DFA. Cluster analysis also revealed that sites that were geographically close were not more similar to one another than they were to other sites of the same land-use type.

Tukey’s test revealed that the four land-use types differed significantly in terms of several habitat features (Table 4). As monocultures, agricultural sites were distinct from all other sites (Tables 2 and 4).

Table 4
Results from Tukey’s test on habitat features among land-use types^a

Habitat feature	MSE ^b	Agricultural	Residential	Industrial	Desert
% Cover native trees	2.279	a	b	b	b
% Cover exotic trees	0.098	a	b	a	a
% Cover native shrubs	35.095	a	b	bc	c
% Cover exotic shrubs	0.254	a	b	b	a
% Cover cactus	2.433	a	b	b	b
% Cover grass (lawn)	68.552	a	b	b	a
% Cover herbaceous	57.686	a	b	b	b
% Cover bare soil	147.044	a	b	c	c
% Cover rocks	35.732	a	a	b	b
% Cover gravel	14.832	a	b	b	c
% Cover concrete	27.092	a	b	b	a
% Cover buildings	15.343	a	b	a	a
% Cover swimming pools	0.025	a	b	a	a

^a Comparisons are made across columns within a row; row entries represented by the same letter are not significantly different (d.f. = 10, $\alpha = 0.05$). Percent cover values were arcsine-transformed for analysis.

^b Mean squared error.

Residential sites more closely resembled industrial sites than they did the other land-use types, particularly with respect to the presence of exotic shrubs and grass (Tables 2 and 4). Both residential and industrial sites were also distinguished by having concrete and/or built structures present within 25 m of each site. Residential sites had the greatest diversity of habitat features (Table 2). No exotic plants were found in the desert remnant sites we sampled (Table 2).

This dissimilarity in terms of habitat features was reflected in dissimilarity of arthropod community composition with land use. In comparing community similarity among the four replicates of a given land-use type, average MI values generally were high, with the median value being 0.84 (Table 5). However, when springtails, mites, and ants were excluded from analysis, community similarity decreased sharply, with a median of 0.34. Similarly, in comparing among the four land-use types, MI values were high when springtails, mites, and ants were included in analysis (median = 0.66) and low when these taxa were excluded (median = 0.34). As per our initial expectations, agricultural and remnant desert communities were the most dissimilar (Table 5).

Community composition varied significantly with land use ($F_3 = 10.18$, $P = 0.0001$; Fig. 5). Predators, herbivores, and detritivores were most abundant in agricultural sites, whereas omnivores were equally abundant in all forms of land use (Fig. 6). CCA revealed that arthropod community composition varied with land use, resulting from taxon-specific responses to habitat structure (percent horizontal ground cover of a variety of natural and anthropogenic features) (Fig. 7). CCA revealed three groupings of habitat structure (and the ground arthropod taxa associated with each): native vegetation, agricultural crops, and features associated with buildings or dwellings (exotic plants, lawn, and gravel; Fig. 7).

Diversity and abundances varied seasonally. Taxonomic richness and abundance of arthropods were greatest in summer, least in winter, and intermediate in spring and autumn (Fig. 8). Richness and abundance tracked temperature but not precipitation (Fig. 8). There were significant correlations between richness and average daily maximum air temperature ($r_s = 0.97$, $P = 0.0001$) and average daily minimum air temperature ($r_s = 0.95$, $P = 0.0001$) but not between richness and average precipitation ($r_s = -0.10$, $P =$

Table 5

MI values for pairwise comparisons of sites and site types, with the three most abundant taxa (springtails, mites, and ants) included and excluded^a

Pair	MI with springtails, mites, and ants included	MI excluding springtails, mites, and ants
<i>Agriculture</i>		
1 vs. 2	0.70	0.33
1 vs. 3	0.64	0.64
1 vs. 4	0.85	0.34
2 vs. 3	0.64	0.60
2 vs. 4	0.57	0.37
3 vs. 4	0.42	0.26
<i>Residential</i>		
1 vs. 2	0.80	0.24
1 vs. 3	0.71	0.05
1 vs. 4	0.84	0.13
2 vs. 3	0.93	0.39
2 vs. 4	0.88	0.32
3 vs. 4	0.94	0.06
<i>Desert remnant</i>		
1 vs. 2	0.97	0.66
1 vs. 3	0.94	0.22
1 vs. 4	0.93	0.71
2 vs. 3	0.98	0.08
2 vs. 4	0.97	0.89
3 vs. 4	0.98	0.13
<i>Industrial</i>		
1 vs. 2	0.82	0.27
1 vs. 3	0.65	0.40
1 vs. 4	0.99	0.32
2 vs. 3	0.93	0.89
2 vs. 4	0.79	0.66
3 vs. 4	0.74	0.63
Agriculture vs. residential	0.89	0.29
Agriculture vs. desert remnant	0.49	0.20
Agriculture vs. industrial	0.58	0.48
Residential vs. desert remnant	0.61	0.24
Residential vs. industrial	0.72	0.51
Desert remnant vs. industrial	0.98	0.39

^a Site names follow Table 1.

0.7613). These relationships held true in all four land-use types (Table 6). The relationships between abundance and maximum temperature ($r_s = 0.47$, $P = 0.0007$), minimum temperature ($r_s = 0.46$, $P = 0.0009$), and precipitation ($r_s = -0.16$, $P = 0.2770$) were similar to those with richness but not as strong. Unlike richness, however, these relationships were not consistent among different land-use types: there were

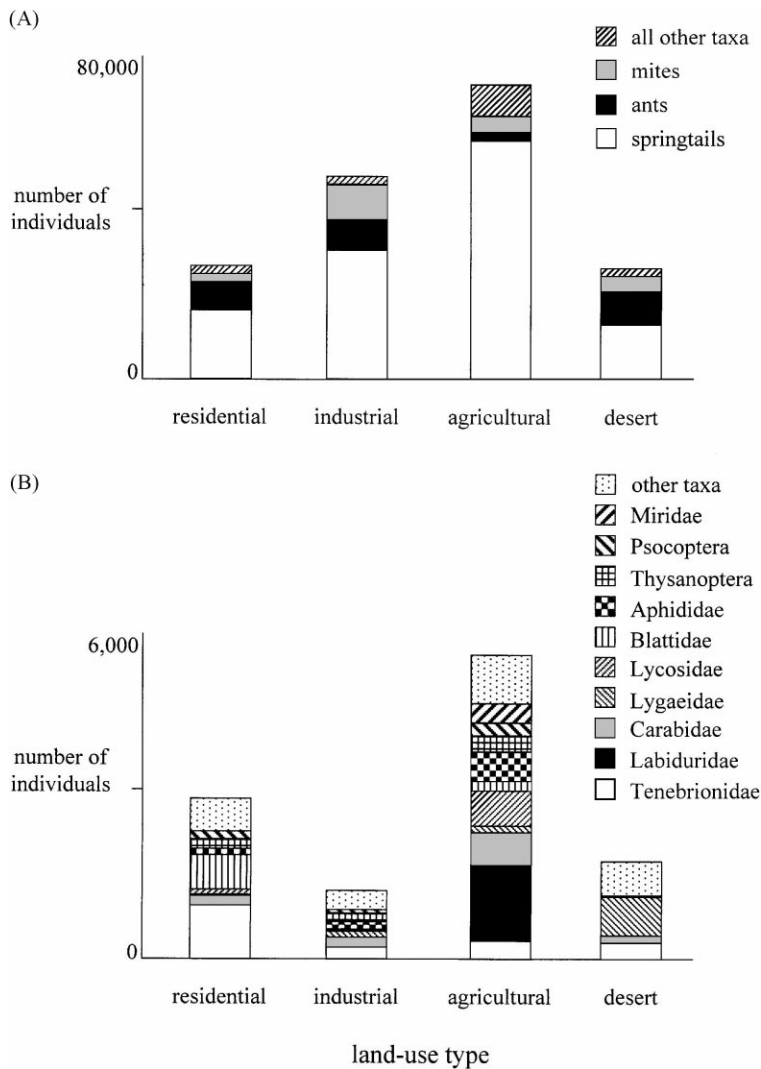


Fig. 5. Stacked bar diagram of taxonomic composition by land-use type, with the three most abundant taxa (Acari, Collembola, Hymenoptera: Formicidae) included (A) and excluded (B). In (B) “other taxa” category consists of taxa representing <3% of total abundance.

significant relationships between abundance and temperature at desert and industrial sites but not at agricultural or residential sites (Table 6).

4. Discussion

One of the primary distinguishing features of an urban ecosystem is the presence of a variety of forms of land use. Arthropod responses to land use may be derived from taxon-specific responses to habitat struc-

tures that are characteristic of each form of land use. Although CCA revealed most taxa to be habitat generalists, it also showed that there are taxa associated with each of the three groupings of habitat features (native, agricultural, and exotic; Fig. 7). Any given form of land use may incorporate any or all of these features. Therefore, it is not necessarily the type of land use per se that drives arthropod community composition: rather, it is the habitat structure present.

Other factors may also influence arthropod community structure, such as climate. For example, arthro-

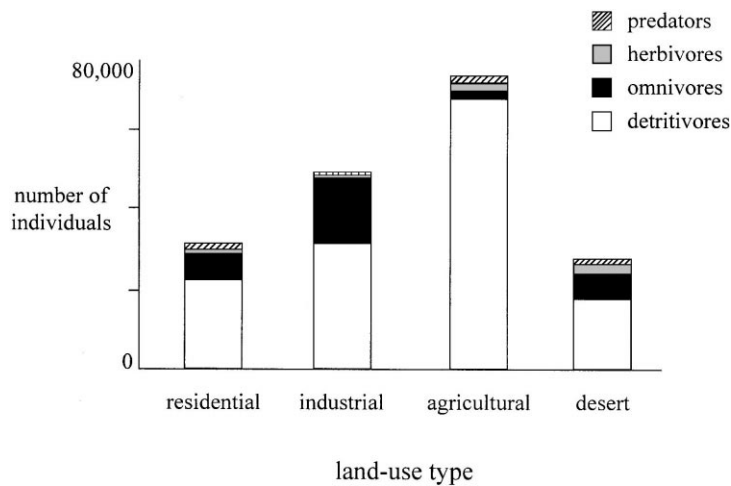


Fig. 6. Stacked bar diagram of trophic structure by land-use type.

pod richness and abundance were influenced by temperature and precipitation. Both richness and abundance corresponded more closely to air temperature than to precipitation, possibly because air temperature can be predicted with a greater degree of accuracy than can precipitation in a desert environment, where both the timing and amount of precipitation are highly variable (Williams, 1979). Alternatively, ectotherms like arthropods necessarily respond strongly to temperature, and changes in activity levels alter an arthropod's probability of capture by a pitfall trap (Southwood, 1966). Because arthropods respond strongly to temperature, this suggests

that the urban "heat island" effect (Kim, 1992) in the Phoenix metropolitan area may impact both arthropod richness and abundance. However, the urban "heat island" effect may be moderated by land use in Phoenix, particularly in those types of land use that receive supplemental watering (i.e., agricultural and residential sites).

Ground arthropod community composition varied with land use. The abundance of springtails, mites, and ants among all forms of land use made them poor indicators of the various potential effects of urbanization. Therefore, future studies on arthropods in urban ecosystems may wish to exclude these taxa if central

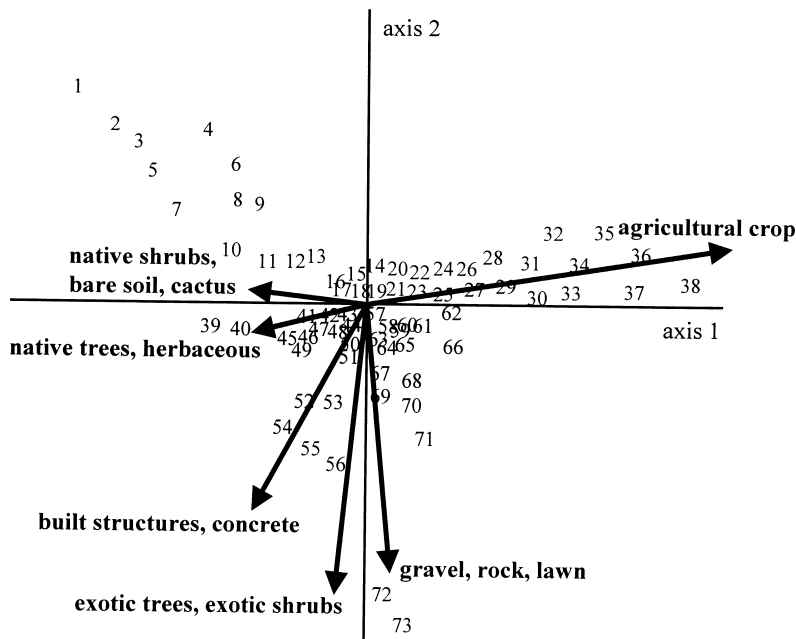
Table 6

Spearman correlations among taxonomic richness, abundance (number of individuals), average daily maximum air temperature (MAX), average daily minimum air temperature (MIN), and average daily precipitation (PPT)^a

Variable, land use ^b	MAX	MIN	PPT
<i>Richness</i>			
Agriculture	0.94 (0.0001)	0.93 (0.0001)	-0.22 (0.4907)
Desert remnant	0.94 (0.0001)	0.93 (0.0001)	-0.08 (0.8028)
Industrial	0.71 (0.0099)	0.65 (0.0224)	-0.18 (0.5779)
Residential	0.76 (0.0040)	0.80 (0.0019)	0.09 (0.7863)
<i>Abundance</i>			
Agriculture	0.11 (0.7292)	0.03 (0.9141)	-0.08 (0.8122)
Desert remnant	0.92 (0.0001)	0.92 (0.0001)	0.04 (0.8883)
Residential	0.71 (0.0092)	0.69 (0.0126)	-0.48 (0.1446)
Industrial	0.31 (0.3191)	0.35 (0.2652)	-0.34 (0.2756)

^a P-values are given in parentheses.

^b "Variable" signifies richness or abundance; "land use" signifies land-use type.



1 Ctenidae	21 Elateridae	41 Acari	61 Acrididae
2 Meinertellidae	22 Thyreocoridae	42 Tingidae	62 Corylophidae
3 Opiliones	23 Pseudoscorpiones	43 Tenebrionidae	63 Aphididae
4 Lygaeidae	24 Nitidulidae	44 Theridiidae	64 Psocoptera
5 Scorpiones	25 Labiduridae	45 Histeridae	65 Cucujidae
6 Buprestidae	26 Membracidae	46 Thomisidae	66 Staphylinidae
7 Oonopidae	27 Labiidae	47 Salticidae	67 Pselaphidae
8 Caponiidae	28 Miridae	48 Formicidae	68 Nabidae
9 Melyridae	29 Rhopalidae	49 Gryllidae	69 Dictynidae
10 Lepismatidae	30 Lathridiidae	50 Thysanoptera	70 Delphacidae
11 Mutillidae	31 Coccinellidae	51 Cicadelliidae	71 Aleyrodidae
12 Clubionidae	32 Anthocoridae	52 Enicocephalidae	72 Scytodidae
13 Chrysomelidae	33 Reduviidae	53 Embiidina	73 Blattidae
14 Termitidae	34 Anthicidae	54 Chilopoda	
15 Carabidae	35 Cicindelidae	55 Oecobiidae	
16 Araneidae	36 Curculionidae	56 Psyllidae	
17 Mantidae	37 Scarabaeidae	57 Gnaphosidae	
18 Collembola	38 Lycosidae	58 Plectreuridae	
19 Linyphiidae	39 Solifugae	59 Cydidae	
20 Gryllacrididae	40 Pholcidae	60 Coccidae	

Fig. 7. CCA ordination diagram for ground arthropods as related to habitat variables. Numbers represent taxa (coded in figure legend), with each number representing a maximum-likelihood estimate of the mode of abundance as a function of environmental gradients (ter Braak, 1986). Arrows represent linear combinations of environmental variables, denoted with bold text (arcsine-transformed percent ground cover of lawn, bare ground, gravel, concrete, native trees, native shrubs, exotic trees, exotic shrubs, cactus, herbaceous plants, rock, agricultural crops, and built structures (e.g., buildings, swimming pools)). The location of each number relative to the arrows indicates the habitat characteristics associated with that taxon (Palmer, 1993; Poulin et al., 1993). Arrow length indicates the correlation between habitat variables and the ordination axes and thus assesses the importance of habitat variables in predicting the pattern of variability in the CCA model (ter Braak, 1986). Arrow direction indicates the strength of correlation with the axes (with a small angle between arrow and axis indicating high correlation). The angle between arrows indicates the correlation between variables (with a small angle indicating high correlation). Monte Carlo randomization: axis1 eigenvalue = 1.415, $P = 0.0390$, 45.8% variance explained; axis 2 eigenvalue = 0.632, $P = 0.0480$, 20.4% variance explained. Note that there are three groupings of habitat features: native plants (top left), agricultural crops (top right), and features associated with buildings or dwellings (bottom center).

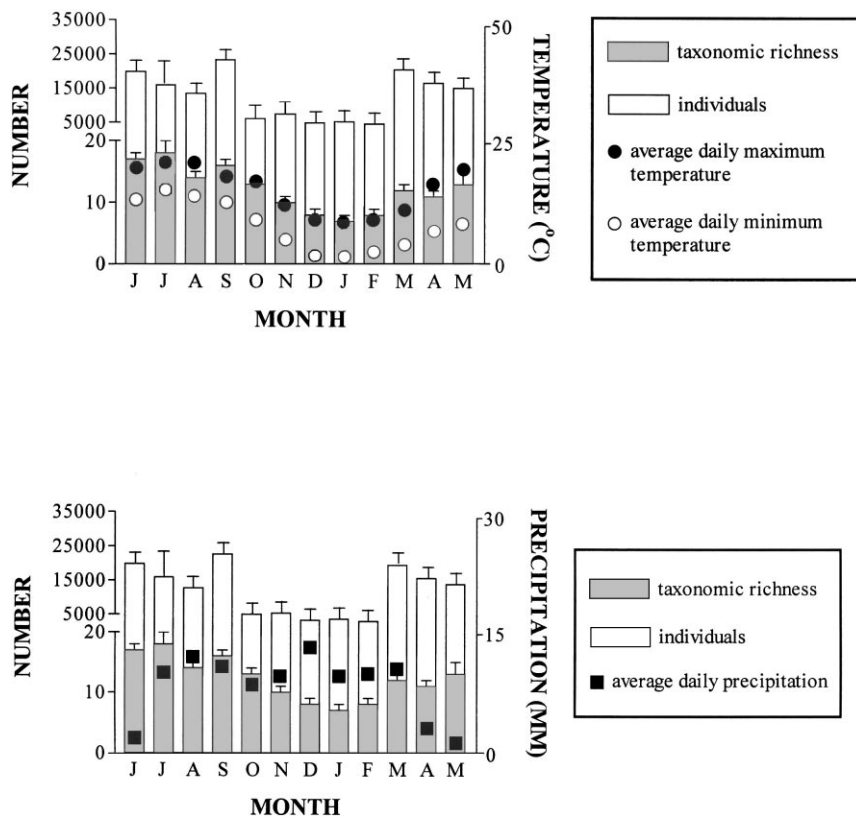


Fig. 8. Mean (+S.E.) taxonomic richness and abundance plotted against average minimum and maximum air temperatures in °C and precipitation in millimeter by month (abbreviated by first letter) for the duration of our study. Note that X-axis runs from June 1998 to May 1999 (the duration of our study) rather than the customary January–December. Richness is depicted as shaded bars and abundance as white bars, left-hand Y-axis, in both upper and lower graphs. Average daily maximum air temperature is depicted as filled circles, right-hand Y-axis (upper graph); average daily minimum air temperature is depicted as open circles, right-hand Y-axis (upper graph). Average daily precipitation is depicted as filled squares, right-hand Y-axis (lower graph).

research questions focus on diversity and rarity. However, the sheer abundance of these taxa indicates that they are tolerant of urbanization in its varied forms. Hence, studies that want to investigate adaptations to urbanization may consider focusing on these taxa. In contrast to these common taxa, we found 14 taxa that are indicative of each of the four forms of urban land use (indicated in Appendix A). These 14 taxa may be particularly sensitive to change and thereby act as indicators of urbanization even before urban development is evident. For example, locations on the fringes of urban areas may not be developed per se but may be affected nonetheless by proximity to urban sources of disturbance or pollution; these latent effects of urbanization may bring about changes to arthropod popu-

lations even before urban development occurs (see also Rees, 1996; Wackernagel and Rees, 1997).

The spatial heterogeneity of land-use types in the Phoenix, AZ, metropolitan area contributes to an overall diverse arthropod fauna in the city environs. The implication is that local arthropod biodiversity may be supported if spatial heterogeneity in terms of land use is incorporated into future urban development. However, some arthropods do well in urban environments (roaches being a notorious example), whereas other taxa do not (e.g., parasitoids; Sawoniewicz, 1986; Denys and Schmidt, 1998), and still other taxa (e.g., springtails, mites, and ants) occur in both urban and rural environments (Czechowski and Mikolajczyk, 1981; Blair and Launer, 1997; McIntyre,

2000). Even though the numbers of taxa captured among the four land-use types were similar, the community composition among the four types differed. The issue of “species quality” as compared to “species quantity” (using the terminology of Murphy (1989)) is of particular concern in urban ecology (Jensen, 1998; Kloor, 1999), because differences in arthropod assemblages may translate into differences in ecosystem functioning with land use (Kruess and Tschardtke, 1994). Arthropods play key roles in a variety of ecosystem functions, including nutrient cycling (Klein, 1989; Crist and Wiens, 1996; Lawton et al., 1996), organic matter decomposition (Siepel and Maaskamp, 1994; Naeem et al., 1995), pollination (Kevan, 1975, 1991; LaSalle and Gauld, 1993), and soil aeration (Folgarait, 1998; de Bruyn, 1999). For example, we uncovered differences in trophic webs with land use (predators, herbivores, and detritivores were most abundant in agricultural sites, whereas omnivores were equally abundant in all forms of land use), which suggests that there may be differences in nutrient cycling with land use in Phoenix. How these roles vary with urban development merits further research.

Future research should also concentrate on spatially explicit, landscape-level effects of land use (e.g., patch size, aggregation, isolation, and context), differences in ecosystem functions with land use, and the roles of arthropods in these functions. Habitat islands separated by as little as 500 m may be effectively isolated for some arthropods (Kruess and Tschardtke, 1994). A great deal of research is needed to make urban biodiversity conservation a reality, including research on the size, shape, and spacing of various forms of land use. Already a pressing concern, this issue will become even more so in the future (Pyle et al., 1981; Clark and Samways, 1997). The world’s annual human population currently increases by approximately 90 million people each year (Matson, 1990), expanding urbanization in both range and magnitude. Therefore, research on organisms in urban environments must begin now in earnest.

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Appendix A. List of ground arthropod taxa captured. Orders listed alphabetically in bold, Families (insects and spiders only) indented. Taxa denoted with an asterisk (*) were represented by a single individual. Taxa denoted with “D” were found only at the desert sites, “A” only at agricultural sites, “R” only at residential sites, and “I” only at industrial sites

Acari

Araneae

- Araneidae
- Caponiidae
- Clubionidae
- Ctenidae*^D
- Dictynidae
- Gnaphosidae
- Linyphiidae
- Lycosidae
- Oecobiidae
- Oonopidae^D
- Pholcidae
- Plectreuridae
- Salticidae
- Scytodidae^R
- Theridiidae
- Thomisidae

Blattaria

- Blattidae

Chilopoda**Coleoptera**

Anthicidae
 Buprestidae^D
 Carabidae
 Chrysomelidae
 Cicindelidae
 Coccinellidae
 Corylophidae
 Cucujidae^R
 Curculionidae
 Elateridae
 Histeridae
 Lathridiidae
 Melyridae
 Nitidulidae
 Pselaphidae
 Scarabaeidae
 Staphylinidae
 Tenebrionidae

Collembola**Dermaptera**

Labiduridae
 Labiidae

Embiidina**Hemiptera**

Anthocoridae^{*D}
 Cydnidae
 Enicocephalidae^{*A}
 Lygaeidae
 Miridae
 Nabidae
 Psyllidae
 Reduviidae
 Rhopalidae
 Thyreocoridae^I
 Tingidae

Homoptera

Aleyrodidae

Aphididae
 Cicadellidae
 Coccidae
 Delphacidae
 Membracidae^A

Hymenoptera

Formicidae
 Mutillidae

Isoptera

Termitidae^I

Mantodea

Mantidae

Microcoryphia

Meinertellidae^D

Opiliones**Orthoptera**

Acrididae
 Gryllacrididae
 Gryllidae

Pseudoscorpiones^{*D}**Psocoptera****Scorpiones^D****Solifugae****Thysanoptera****Thysanura**

Lepismatidae

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