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Trophic Dynamics in Urban Communities

STANLEY H. FAETH, PAIGE S. WARREN, EYAL SHOCHAT, AND WENDY A. MARUSSICH

Human activities dramatically change the abundance, diversity, and composition of species. However, little is known about how the most intense human activity, urbanization, alters food webs and trophic structure in biological communities. Studies of the Phoenix area, situated amid the Sonoran Desert, reveal some surprising alterations in the control of trophic dynamics. Species composition is radically altered, and resource subsidies increase and stabilize productivity. Changes in productivity dampen seasonal and yearly fluctuations in species diversity, elevate abundances, and alter feeding behaviors of some key urban species. In urban systems—in contrast to the trophic systems in outlying deserts, which are dominated by limiting resources—predation by birds becomes the dominant force controlling arthropods on plants. Reduced predation risk elevates the abundance of urban birds and alters their foraging behavior such that they exert increased top-down effects on arthropods. Shifts in control of food web dynamics are probably common in urban ecosystems, and are influenced by complex human social processes and feedbacks.

Keywords: community, food webs, trophic dynamics, species composition, urban ecosystems

Ecologists have long debated what factors control the trophic (feeding) structure and function of ecosystems. This is more than just a matter of determining "who eats whom"; ecologists have pondered whether there are fundamental rules for determining (a) how many trophic levels an ecosystem can support, (b) how much primary production is consumed by herbivores, and (c) whether resources from the bottom of the food chain, or consumers from the top, control biomass, abundance, and species diversity in food webs. These questions are not only fundamental to ecology but essential for conservation and management. For example, the loss of a top predator in a food web that is largely controlled by top-down forces may drastically alter biodiversity and ecosystem function (e.g., nutrient cycling), whereas the same loss may have little effect in a resource-controlled (i.e., bottom-up) food web.

To answer these questions, ecologists have expended an enormous effort to understand the relative importance of predation or parasitism (and, to a lesser extent, mutualism) and competition for resources in trophic organization. Three basic models of control of trophic structure have emerged from this endeavor. The first of these, the energetic model of food webs, holds that energy supply (from the bottom of food webs), in concert with the relative efficiencies of consumers, limits the number of trophic levels and the relative biomass of each level in natural ecosystems (Lindeman 1942). The second model, commonly known as the "green world" hypothesis (Hairston et al. 1960), states that predators and parasites exert top-down control on herbivore populations. According to this model, herbivores do not generally compete with each other, and plant resources are not limiting because herbivore population densities remain low as a result of top-down control. The third model (Menge and Sutherland 1987) hypothesizes that the relative effects of predation on species diversity vary as a function of environmental stress (e.g., exposure, desiccation, extreme temperatures) and productivity. Specifically, the Menge–Sutherland model suggests that predation should be more important at low and intermediate levels of stress, because high stress limits the abundance of predators more than it limits herbivore competitors. Competition for resources should be more important at high levels of stress (and low levels of productivity). Various modifications and elaborations of these three basic models of food webs and trophic structure have proliferated in the past several decades (Oksanen et al. 1981, Power 1992).

Empirical tests of the food web models, and modifications thereof, have been conducted mostly in non–human-dominated ecosystems ranging from marine environments to freshwater lakes and streams, tundra, deserts, forests, and grasslands, each test often producing a different answer (Connell 1983, Schoener 1983, Sih et al. 1985). Empirical tests and the development of theory for food web dynamics have historically involved human-dominated ecosystems, such as agroecosystems (Rosenheim 1998), or recovering agricul-

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tural settings ("old fields"; Schmitz 2003). However, trophic organization has not been well studied in urban areas, the most rapidly expanding and human-altered habitat type on Earth (McKinney 2002).

Although population and community ecologists have generally avoided cities in lieu of more pristine and "natural" habitats, there are compelling reasons to intensify ecological studies in urban areas. Urbanization is a dominant demographic trend that transforms land usage worldwide and radically changes ecological patterns and processes (Vitousek et al. 1997, Collins et al. 2000, Grimm et al. 2000, Alberti et al. 2003). By 2007, the majority of the world's population will live in cities for the first time in human history (McKinney 2002). Urbanization interacts with global change and plays a central role in the alteration of global biogeochemical cycles, in the reduction of biodiversity due to habitat fragmentation and introduction of exotic species, and in land-use and land-cover changes that extend far beyond the city's boundaries (Collins et al. 2000, Alberti et al. 2003). Thus, many apparently pristine and "natural" areas have already been, and will increasingly become, part of the ecological "footprint" of urban areas (McDonnell and Pickett 1993, Wackernagel and Rees 1996, Dobson et al. 1997, Vitousek et al. 1997, Luck et al. 2001, Grimm et al. 2003).

Understanding the structure and function of food webs in urban settings is essential because, like the human population, Earth's other species are now increasingly found in, or influenced by, urban areas (McKinney 2002). Critical to the growing conservation efforts directed at urban areas (Barker 2000) is knowing how productivity is related to diversity, how species interactions that comprise food webs are maintained, and what controls the number of trophic levels and the diversity within them. All species interact with one or more other species in food webs via competition, predation, parasitism, or mutualism, and thus conservation efforts are unlikely to succeed unless these complex food web interactions and the ways human activities alter them are understood. Furthermore, food webs in cities provide many direct and indirect ecosystem services (Alberti et al. 2003), such as the pollination of home garden plants, the recycling of limited nutrients, the degradation of wastes and pollutants, the control of pests by predators and parasites, and the aesthetic value of wildlife and green spaces. Maintenance and management of these ecosystem services requires a basic knowledge of how urban food webs function and persist.

The urban food web

Primary productivity forms the foundation for food webs and trophic interactions in all ecosystems. The Central Arizona–Phoenix Long Term Ecological Research (CAP LTER) group has been studying the interactions of human activities with biodiversity, nutrient cycles, and productivity in the Phoenix, Arizona, metropolitan area since 1998 (Grimm et al. 2000). Like many cities in the US Southwest, the Phoenix urban area, comprising the central Arizona–Phoenix metropolitan area and associated suburbs and municipalities (referred to hereafter as the CAP LTER study area), is rapidly expanding in both area and population. The city is situated amid the Sonoran Desert, and urbanization has occurred on two main fronts: (1) conversion of agricultural lands (which were largely undisturbed desert about 100 years ago) into suburbs and industrial land uses, and (2) outward expansion of suburban housing into the fringe desert surrounding the city (Gober et al. 1998). In the Sonoran Desert, plant productivity is limited primarily by water availability; precipitation is low and average temperatures are high. Limited water availability coupled with very high temperatures, especially during the early summer months, results in high evapotranspiration rates and generally stressful conditions for plants and associated consumer communities. Light is not generally limiting, and nutrients do not become limiting until water availability is well beyond ambient levels (Stabler and Martin 2004).

From long-term and ongoing studies at the CAP LTER site, we know that human activity has tremendous effects on plant productivity in the Phoenix metropolitan area. Not surprisingly, plant productivity is much higher in agricultural areas, and areas of mesic residential land use (figure 1), than in desert remnants (Sonoran Desert fragments within the urban matrix) and outlying, contiguous deserts (Stabler and Martin 2004). However, even native Sonoran Desert plants and nonnative desert plants (i.e., those that are arid-adapted but not endemic to the Sonoran Desert) are generally much more productive in urban environments than in outlying or remnant deserts (Martin and Stabler 2002, Stabler and Martin 2004). This unanticipated outcome stems from human behaviors at various organizational levels (governmental to individual), which, in turn, stem from human perceptions, values, and socioeconomic processes (Hope et al. 2003). In short, humans increase water usage in xeriscapes to keep desert plants "green" and growing, especially during dry periods when desert plants typically senesce (Martin 2001, Stabler and Martin 2004).

Not only is plant productivity generally higher in the urban CAP LTER study area than in the outlying desert, it is also more uniform over time. Seasonal fluctuations in precipitation drive two distinct seasonal pulses in productivity in the desert: in the spring, after winter rains originating from westerly fronts, and in late summer, after cyclonic cells moving from the south (Brazel and Ellis 2003). Intervening periods are usually extremely dry. Furthermore, annual precipitation, and thus productivity, varies across years, especially during wetter El Niño events and more recent (since 1999) drought cycles (Brazel and Elllis 2003, Shochat et al. 2004a). However, human activities in the Phoenix metropolitan area have reduced this intra- and interannual variation (figure 2). Higher and more consistent productivity alters the patterns of seasonal and annual diversity and abundance for major animal taxa. Productivity changes, coupled with direct human activities, set the stage for modifications in trophic structure and dynamics.

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Figure 1. Photograph of the Central Arizona–Phoenix Long Term Ecological Research study area, showing Indian Bend Wash, a former intermittent stream channel that has been modified to include permanent lakes and a highly productive riparian zone, with surrounding suburban and light industrial land use. Photograph: Stan Faeth.

Urban changes in producer and consumer species

The Phoenix metropolitan area, like other urban ecosystems (McKinney 2002; table 1), has experienced radical changes in the diversity and abundance of plant, herbivore, detrivore, predator, and parasite species. In general, the species richness of plants (Hope et al. 2003), herbivorous arthropods, predatory arthropods, and detrivores (McIntyre et al. 2001) has remained about the same or even increased in some cases (e.g., with the introduction of exotic plant species), whereas the richness of vertebrate species (birds, amphibians, reptiles, and mammals) has generally decreased (Sullivan and Flowers 1998). However, human activities have dramatically altered the relative abundance and composition of species. For example, the relative abundance of some native and nonnative species has greatly increased, apparently at the expense of more specialized species, in the following groups: generalist bird species, generalist ground arthropods (e.g., ants, springtails, and mites), plant-feeding arthropods (e.g., aphids, whiteflies), generalist pollinating arthropods (e.g., honeybees), jumping spiders (Lycosidae), and fence lizards (McIntyre et al. 2001, Shochat et al. 2004a). Urban expansion in the Phoenix metropolitan area, as in other southwestern urban areas, is recent compared with that in most US cities. Thus, many species that are prone to local extinction (e.g., herpetofauna) are still present, but greatly reduced, in desert remnants, and their richness is likely to decline in the future (Sullivan and Flowers 1998). Most of the anthropogenic changes in species composition have been indirect. Alterations have resulted mainly from historical changes in land use rather than intentional human manipulation or extirpation of species. Desert habitats were converted to agricultural and, more recently, to suburban and industrial land uses (Gober et al. 1998). In comparison with the original desert, each of these land uses is associated with increases in resources, especially water, that augment and modulate productivity. For example, spider diversity is generally reduced in the Phoenix metropolitan area, but certain families, which are typical of mesic habitats (e.g., Lycosidae and Linyphiidae; see Toft 1999), have become dominant in highly productive areas of mesic yards and agricultural fields (Shochat et al. 2004a). Shifts in dominance and species composition of arthropod species with land-use changes are also found in other human-dominated areas in the southwestern United States (Longcore 2003).

Human activities have directly altered producer and consumer species through the elimination of native species and the introduction of nonnatives (table 1, figure 2). However, the repercussions for trophic dynamics are not easily predictable, because introductions and extinctions are not usually "in kind" in terms of trophic interactions (Crooks and Soulé 1999). For example, some native predators of birds are rare in the city (e.g., raptors), but domestic cats have been introduced. Domestic cats have their greatest impact on fledgling birds (e.g., Clarke and Pacin 2002); adult birds in Phoenix appear to experience reduced top-down control because of missing top predators, such as raptors (Shochat 2004, Shochat et al. 2004b). Likewise, overall plant productivity and flowering have greatly increased in the CAP LTER study area, with increased resources for generalist pollinators

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Table 1. Common features of urban ecosystems and their projected consequences for food webs.

Feature	Effects on food webs
Fragmentation (including remnants or reconstructed original habitats)	Rapid changes in species composition Increased spatial heterogeneity in food web dynamics within cities Remnant food webs that differ from original habitat (figure 4)
Reduction of top predators	Trophic cascades Increased competition and bottom-up control of mesopredators and insectivores Increased top-down control of herbivores by mesopredators and insectivores
Changes in productivity*	Increased or decreased bottom-up control Reduced temporal fluctuations in populations
Changes in stress-related factors* (e.g., temperature, nutrients)	Increased or decreased stress-mediated control Shift to more stress-tolerant or less stress-tolerant producers and consumers
Changes in species composition	Increased or decreased bottom-up and top-down control Change in number of trophic levels Local extinction or addition of interacting species
Human activities (mediated by social and institutional processes and values)	Altered food web structure, control, and dynamics Spatial and temporal scales may supersede those of ecological processes

Asterisk (*) indicates features most likely to vary according to the bioregional context of the city (desert, temperate forest, tropical rainforest, grassland, etc.).

such as honeybees; however, reduction in native Sonoran Desert plant species reduces the richness of pollinating species, especially solitary bees, which typically specialize on Sonoran Desert plants (McIntyre and Hostetler 2001, Minckley and Roulston 2005). In contrast with the situation in many eastern US cities, vertebrate grazers and browsers (such as deer, javelina, lagomorphs, and domestic cattle—the latter present in Arizona since the 16th century) are also largely absent from the built-up landscapes within the Phoenix metropolitan area, and overall vertebrate herbivory on plants has been reduced (figure 2). This trend of reduced vertebrate herbivory, however, could change in the future, if vertebrates such as lagomorphs (e.g., the jackrabbits now found locally in some mesic locations and desert remnants in the Phoenix area) become more abundant while their predators remain absent or rare in urban areas.

Urban environments are characterized by high spatial heterogeneity resulting from varying land use and fragmentation of habitats (table 1; Rebele 1994, Pickett et al. 2001, Jenerette and Wu 2001). In Phoenix, human activities (e.g., fragmentation and varying land use) have virtually eliminated spatial autocorrelation above the house-plot scale for key soil resources such as nitrogen and phosphorus, and within plots, plant species richness can vary by an order of magnitude across the urban matrix (Hope et al. 2003). Variation in resource levels and habitat structure leads to variation in levels of diversity for other taxa as well (McIntyre et al. 2001). The extreme heterogeneity of habitat structure can be disruptive for many far-ranging animals (Crooks 2002) and can render tenuous any predictions of control of trophic structure. For example, Patten and Bolger (2003) found that fragmentation of urban coastal shrub habitats in southwestern California had differential effects on predator control of ground-nesting and shrub-nesting birds. Although snake abundance was the best predictor of nest failure of the ground-nesting birds, and snake abundance decreased with fragmentation, the ground-nesting species were nevertheless more negatively affected by fragmentation than were shrub-nesting species. Other factors, such as dispersal, apparently reduce success in fragmented habitats. Patten and Bolger (2003) concluded that the strength of top-down control across fragmented landscapes is difficult to predict without knowing in detail the responses of individual predator and prey species to fragmentation. In general, spatial heterogeneity is likely to have profound effects on trophic structure and dynamics in cities, and we expect that trophic dynamics are much more variable spatially in urban areas than in less human-dominated environments (table 1).

Dynamics of interactions between urban birds, insect herbivores, and plants

Because of the complexities inherent in most food webs, we can only roughly estimate the dynamics of trophic relationships for the urban system in this study (figure 2). However, one major component of the Phoenix area's urban trophic system—the segment composed of plants, insect herbivores, and their natural enemies—has been studied in some detail through observations and manipulative experiments, and has revealed some surprising differences from the outlying desert habitats (figure 3).

Urban bird communities exhibit high population densities and low species diversity compared with those in desert habitats (Germaine et al. 1998, Mills et al. 1989, Green and Baker 2003). This trend of lower population density and higher richness in less urbanized rural or wildland habitats is also found in cities in other biomes (Marzluff et al. 2001, McKinney 2002). Recent experimental studies of foraging decisions at artificial food patches indicate that squirrels in eastern US cities (Bowers and Breland 1996) and urban birds in the CAP LTER study area (Shochat et al. 2004b) alter foraging behavior because of reduction in predation risk and increased competition caused by their very high densities. These studies used giving-up densities (GUDs), or the food left over in a patch after a foraging bout, as a measure of the foragers' perception of foraging costs and predation risk (see Shochat et al. 2004b). Squirrel foraging behavior changed

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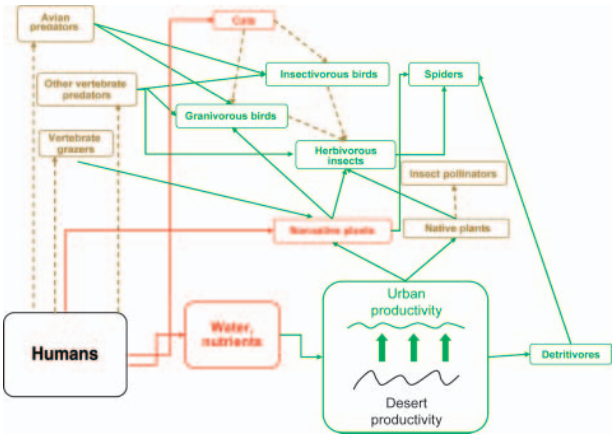


Figure 2. The food web in the Phoenix, Arizona, metropolitan area. Human activity has directly increased available resources, particularly water (shown in red), which has increased and stabilized productivity. This human activity, coupled with other direct effects, such as the introduction of domestic cats (shown in red), and indirect effects, such as the reduction of other vertebrate predators (shown in brown), has increased the abundance of some biotic groups either directly (red solid arrows) or indirectly (green solid arrows), while decreasing others (brown dashed arrows).

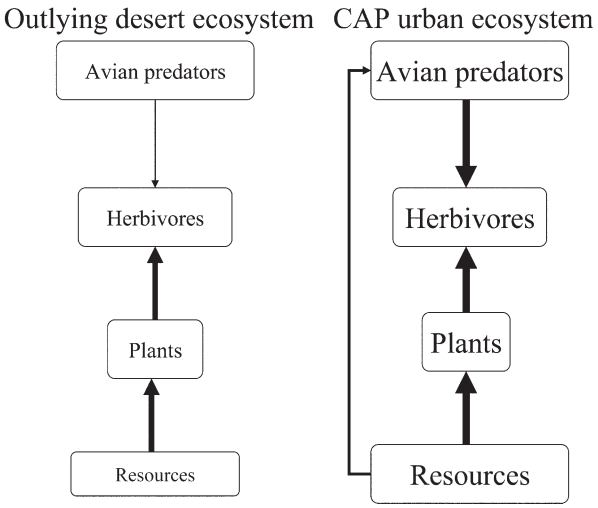


Figure 3. Comparison of trophic dynamics of the central Arizona–Phoenix (CAP) urban ecosystem and the outlying Sonoran Desert ecosystem. In the background desert, bottom-up or resource-based forces dominate the food web, but in the urbanized region, top-down or predatory forces combine with bottom-up forces to control trophic dynamics. Size of typeface in boxes reflects relative differences in biomass; width of arrows indicates relative importance of linkages in each ecosystem.

along 78 forest–rural–urban gradients in Virginia (Bowers and Breland 1996). In the forest, GUDs are higher because of increased predation risk, but in the city, where predation is relaxed, GUDs for squirrels are relatively low owing to competition (Bowers and Breland 1996). The CAP LTER experiment likewise showed that top-down control of adult birds via predation is stronger in outlying desert habitats than in the city (Shochat 2004, Shochat et al. 2004b). In the city, bottom-up competition for a higher and more consistently available food supply by highly efficient urban specialists (e.g., house sparrows and doves) becomes more intense (Shochat 2004, Shochat et al. 2004b). These urban birds are likely to outcompete and exclude native species, thus reducing diversity (Shochat 2004, Shochat et al. 2004b). In general, the absence or reduction of predators and the increased and predictable resources in urban areas may lead to shifts from top-down to bottom-up control of some vertebrate consumers (table 1).

The increase in bird densities in the Phoenix area translates into stronger top-down control of insects feeding on plants in urban areas, although insect abundances are also boosted to higher baseline levels by bottom-up or resource-based forces (figure 3). A long-term experiment, currently in progress in the CAP LTER study area, uses a common Sonoran Desert plant, brittlebush (*Encelia farinosa*), which is also commonly used in urban landscapes. This experiment consists of 40 brittlebush plants at each of three different sites: a mesic suburban yard and a desert remnant within the city, and a contiguous Sonoran Desert site outside the city. Treatments include the exclusion of avian predators (via netting), the exclusion of ground-dwelling predators (via metal flashing), and supplemented water, as well as the corresponding nontreatments (i.e., no cage, no flashing, no supplemented water). The experiment employed three different habitats in a $2 \times 2 \times 2$ factorial design (with five replicates of each treatment at each site). Because this is a long-term, ongoing experiment, we report here results only from four completed sampling periods in the first year of the experiment (2003), and caution that final outcomes could change as the experiment progresses. However, to our knowledge, no other experimental studies have addressed this important component of the urban food web.

Insect herbivores significantly increased in urban areas when birds were excluded, but not in desert areas, although herbivores were already more abundant in urban areas because of higher productivity (figure 4). Insect herbivores increased when water was supplemented in the outlying desert area, but not when it was supplemented in the desert remnant or in the highly modified human habitat (the suburban yard) within the city. Exclusion of ground-dwelling predators had no effect on herbivores in any of the three habitats. These results suggest more top-down control from birds in urban areas and more resource-based, or bottom-up, control of insect herbivores in outlying deserts.

Bird predation is also important in urban desert remnants (figure 4), suggesting that the intensity of bird predation in more mesic habitats spills over into nearby desert remnants that are embedded in the urban matrix. In terms of food web

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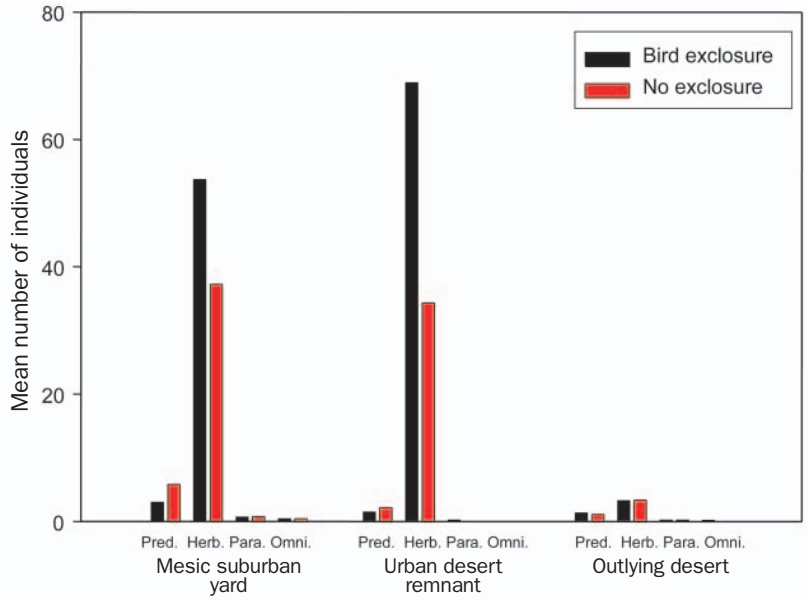


Figure 4. When birds are excluded from brittlebush (*Encelia farinosa*) in mesic suburban yards and in desert remnants within the urban Central Arizona–Phoenix Long Term Ecological Research (CAP LTER) study area, herbivores (herb.), which are already at higher abundances because of increased productivity, increase even more, indicating top-down control by insectivorous birds. Exclusion of birds has no effect on arthropod predators (pred.), parasites (para.), or omnivores (omni.). Exclusion of birds has no effect on herbivores in outlying Sonoran Desert habitats, suggesting less top-down control than in the CAP LTER area.

dynamics, desert remnants appear to function more like urban mesic habitats than their outlying Sonoran Desert counterparts. This is true also of seasonal plant-associated arthropod abundances (figure 4), diversity, and trophic structure. If this pattern of trophic dynamics and structure holds, there are important conservation implications. Preservation of natural remnants of vegetation within urban matrices does not guarantee that plant-associated arthropods and trophic structure and dynamics parallel more contiguous natural areas. Crooks and Soulé (1999) found similar changes in trophic dynamics in coastal shrub habitat surrounded by urban areas. Likewise, Shochat and colleagues (2004a) found that the species diversity and composition of spiders in xeriscaped yards (yards with xeric-adapted plants, both endemic and nonnative) in the CAP LTER study area more closely resembled areas of industrial land use than they did desert remnants or the outlying desert. Thus, human-constructed, urban desert habitats, like preserved desert remnants, fail to mimic the trophic structure of outlying desert habitats. Similar conclusions hold for restored coastal sage scrub habitats in southern California (Longcore 2003).

Conventional ecological theory of food webs predicts that higher resource abundances and reduced diversity of avian predators should result in more bottom-up control of plant arthropods in urban areas. Plentiful resources, and the associated reduction in stress due to increased humidity and water availability (Menge and Sutherland 1987) and declines in predators (Hairston et al. 1960), would suggest that arthropods in most urban systems are controlled through resource-based competition or bottom-up forces. Higher and more consistent levels of resources, however, also amplify bird abundances. Birds become more efficient and intensive predators of arthropods in urban areas (Shochat 2004). Since bird species that forage on arthropods, either as a primary food source or secondarily during the breeding season, thrive in other cities (see Marzluff et al. 2001), these results may be general to other urban ecosystems. Both herbivore and bird species abundances increase and stabilize in urban habitats. However, further increases in bird abundances appear limited by competition for resources (Shochat 2004), whereas plant-dwelling arthropods appear to be limited by increased predation from birds. This combination of bottom-up control (for birds) and top-down control (for arthropods) contrasts sharply with the less human-dominated habitats into which the Phoenix metropolitan area is rapidly expanding (figure 2). Whether increased top-down control of arthropods through increased abundance of birds is common to other urban areas (e.g., Marzluff et al. 2001) awaits similar controlled experiments.

Urban trophic processes are indirectly affected by human social processes and decisionmaking (table 1). We have already noted that human-mediated subsidies (e.g., water and nutrients) generate higher, more stable rates of plant productivity than those in the surrounding desert (Martin and Stabler 2002), thereby affecting both arthropod and avian densities (Shochat 2004). Within the city, however, provision of these subsidies varies with human socioeconomic status and lifestyle factors, as well as neighborhood age (Hope et al. 2003, Martin et al. 2004a). Furthermore, the design of residential plant communities varies considerably with neighborhood socioeconomic factors and cultural composition in the Phoenix metropolitan area (Martin et al. 2004b), as in other cities (Whitney and Adams 1980, Fraser and Kenney 2000, Hope et al. 2003). Humans also affect predator densities by maintaining populations of domestic cats (Crooks 2002); ownership of outdoor cats is correlated with factors such as urban versus rural lifestyle, type of housing, and, to a lesser extent, neighborhood socioeconomic status (Lepczyk et al. 2004). These indirect human impacts contribute to the extreme spatial heterogeneity of urban environments (Rebele 1994, Pickett et al. 2001, Hope et al. 2003). In the Phoenix metropolitan area, one outcome of direct and indirect human impacts is that bird communities in neighborhoods of higher income and social status more closely resemble native bird communities than those in lower socioeconomic neighborhoods (Kinzig et al. 2005). On the basis of our experiments, we predict that trophic structure, like community structure, will vary within the city according to socio-

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economic or lifestyle factors. A thorough and predictive understanding of urban trophic dynamics will require an interdisciplinary recognition of the role of humans in urban ecosystems.

Top predators: Further questions

So far, we have focused our discussion of the urban food web on plants, insect herbivores, and the natural enemies of these herbivores. How might this set of dynamics be affected by higher trophic levels, such as mesopredators and top predators? Work by Crooks and colleagues (Crooks and Soulé 1999, Crooks 2002) has shown that coyotes, a top predator, have indirect effects on avian reproductive success in patches of coastal scrub surrounded by residential areas in San Diego, California. Patches without coyotes have lower avian reproductive success, an effect that is mediated by mesopredator release (i.e., higher visitation rates by domestic cats, opossums, and gray foxes, all of which are preyed on by coyotes; Crooks and Soulé 1999). However, Patten and Bolger (2003) indicate that bird responses to urban fragmentation in these coastal scrub habitats are highly species specific, change ontogenetically, and are not predictable on the basis of predator abundance alone. These contrasting findings suggest that the effects of changes in type and abundance of top predators and mesopredators in urban ecosystems will be difficult to predict, even in similar urban settings, and may change over time.

Although top predators are largely absent in the greater Phoenix area, preliminary predator surveys show that coyotes, as well as occasional nesting raptors, are now moving deep into the urban matrix (Diane Hope, Center for Environmental Studies, Arizona State University, Tempe, Arizona, personal communication, 15 October 2004). As the Phoenix urban area matures, increases and additions of top predators such as coyotes may reduce populations of predators on birds, such as domestic cats. If so, then increases in insectivorous birds could cascade to other trophic levels through the intensified predation of arthropods. Furthermore, the richness and abundance of large iguanid lizard and snake species have been greatly reduced in the CAP LTER study area (Sullivan and Flowers 1998), apparently because of loss and fragmentation of habitat, but also because human-introduced dogs and cats prey upon them. If desert snakes and other reptiles (e.g., large lizards) become still less abundant because of human activities, then reptile predation on birds' eggs and nestlings (e.g., Patten and Bolger 2003, Weatherhead and Blouin-Demers 2004) should also diminish, and may contribute to even higher densities of some urban birds and to increasingly altered feeding behaviors. Alternatively, increases in the number of predators of insectivorous birds, such as cats, could reduce the numbers and thus the predatory effect of arthropod-feeding birds, such that the relationship described here between plants, arthropod herbivores, and their natural enemies is radically altered. Like less human-altered habitats, cities undergo successional changes as they age (Collins et al. 2000), and control of trophic structure and dynamics should shift accordingly as the species composition of top predators and mesopredators changes. However, the consequences of these successional and human-mediated changes on trophic dynamics are likely to vary according to the behavior and autecology of the species, the urban settings in which they occur, and human social processes that can alter outcomes.

Trends in urban trophic dynamics

The CAP LTER study area provides one of the more extreme examples of contrasts between trophic dynamics in a relatively harsh, outlying desert environment and in a more benign, productive, and oasis-like urban habitat. As such, observations and experimentation are likely to yield distinct differences in food webs and trophic dynamics between its urban and surrounding native habitats. We might expect comparable effects in other urbanizing arid environments, which constitute a large and growing fraction of cities, especially in the southwestern United States (UN 1996). However, this raises the question: are the shifts in trophic structure and control that we have described for the CAP LTER area applicable to nonarid urban ecosystems, such as those in temperate and tropical habitats? This question can only be addressed with additional observations and experimentation, but we have noted several common features of urbanization and their likely consequences for food web and trophic dynamics (table 1).

The common urban features shown in table 1 are not independent of each other. For example, increased productivity may reduce competition among predators or herbivores, or the reduction of top predators may cascade downward in food webs to increase levels of productivity if herbivore abundances are reduced. Furthermore, human activities, social processes, and institutional decisionmaking can modify all of these features at spatial and temporal scales that overpower biological processes (Kinzig and Grove 2001). Established local food webs can be obliterated instantaneously if a parking lot is constructed or completely reconfigured when native desert or forest is converted into a suburban lawn. In contrast, with the aging of land-use types such as established parks and suburban neighborhoods within cities, trophic dynamics and structure may develop and persist over relatively long time frames, and ecological and even evolutionary processes may play increasingly important roles relative to human activities. In turn, the ecological processes may feed back to human activities, as individuals and social organizations may value and act to maintain recognizable diversity in local food webs.

Nearly all cities have some areas of original or reconstructed wildland habitat in the form of parks, preserves, or undeveloped land. Researchers have traditionally compared the species composition and diversity of these remnants with those of outlying areas to determine the effects of fragmentation (Soulé 1991, Miyashita et al. 1998, Patten and Bolger 2003). Fragmentation often leads to reduced species diversity and altered trophic structure because of local extinctions, which are caused by reduced population sizes, restricted dispersal and mate location, and reduced genetic diversity within species (Lacy 1987). Whereas these processes are also likely to occur in urban remnants (Wandeler et al. 2003), our exper-

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iments on brittlebush suggest that trophic dynamics in urban remnants may be influenced by factors that are unique to cities. For example, trophic dynamics and structure in desert remnants (figure 4) or reconstructed desert habitats (Shochat et al. 2004a) may bear little resemblance in trophic structure to original habitats, even though remnants and reconstructed habitats look similar to wildland habitats. The causes for these differences are not yet known, but they may include a continuous influx of urban adapters (e.g., herbivorous aphids and omnivorous birds) from the surrounding city matrix, differential susceptibility to urban heat island effects (Brazel and Ellis 2003), and increases in atmospheric nitrogen and carbon dioxide (Baker et al. 2001) that alter plant physiology and nutrition.

The challenge for urban ecologists is to ascertain the direct (e.g., fragmentation) and indirect (e.g., altered climate) ways that urbanization influences food web dynamics in both remnant and nonremnant urban habitats, and to incorporate human activities, processes, and feedbacks into studies of urban food webs. One way to accomplish this is adaptive experimentation, in which ecological experimentation and the activities, responses, and modifications of human residents are studied simultaneously (Cook et al. 2004). Just as ecologists once eschewed ecological studies in urban areas for pristine habitats, a complete understanding of urban food webs may require urban ecologists to shift from focusing on remnant habitats within cities to studying human-modified and constructed habitats. These habitats not only increasingly represent the bulk of urban environments but also are likely to modify food web structure and dynamics in the remaining, or reconstructed, original habitats.

Understanding urban trophic dynamics

Our experimental and observational studies are beginning to reveal the mechanisms underlying trophic structure and dynamics in urban ecosystems. It is increasingly clear that urban trophic systems differ radically from the more natural habitats in which they are embedded, although the same processes, such as resource and consumer control, still apply. Urban ecosystems may deviate from conventional expectations derived from empirical and theoretical models of food web structure that are based on non–human-dominated systems. Generally, it appears that urbanization in the Phoenix study area causes shifts from a resource-based or bottom-up controlled system (Lindeman 1942) typical of the Sonoran Desert to a combined bottom-up and top-down model wherein predation becomes increasingly important for some taxa as resources become abundant and predictable. However, outcomes depend heavily on species compositional and productivity changes, spatial heterogeneity, succession, and alterations in behaviors, such as foraging. Human decisionmaking, values, intervention, and social and cultural processes influence all of these aspects, and the ecological processes feed back to human decisionmaking, further complicating trophic dynamics and structure in cities. Future experiments should integrate both ecological and sociological approaches (Grossman 1993, Alberti et al. 2003, Cook et al. 2004) and should incorporate not only remnant but also human-constructed habitats, to more thoroughly investigate trophic dynamics in urban ecosystems.

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