Urban Food Webs: Predators, Prey, and the People Who Feed Them

A prevailing image of the city is of the steel and concrete downtown skyline. The more common experience of urban residents, however, is a place of irrigated and fertilized green spaces, such as yards, gardens, and parks, surrounding homes and businesses where people commonly feed birds, squirrels, and other wildlife. Within these highly human-modified environments, researchers are becoming increasingly curious about how fundamental ecological phenomena play out, such as the feeding relationships among species. While food webs have long provided a tool for organizing information about feeding relationships and energy flows through natural habitats, they have not been applied to urban ecosystems until recently (Faeth et al. 2005).

At a symposium presented at the 2006 Ecological Society of America meeting, 10 speakers assembled to present and discuss "The Urban Food Web: How Humans Alter the State and Interactions of Trophic Dynamics," in a symposium organized by Paige Warren, Chris Tripler, Chris Lepczyk, and Jason Walker. A key feature of urban environments, as described in the symposium, is that human influence may be en-

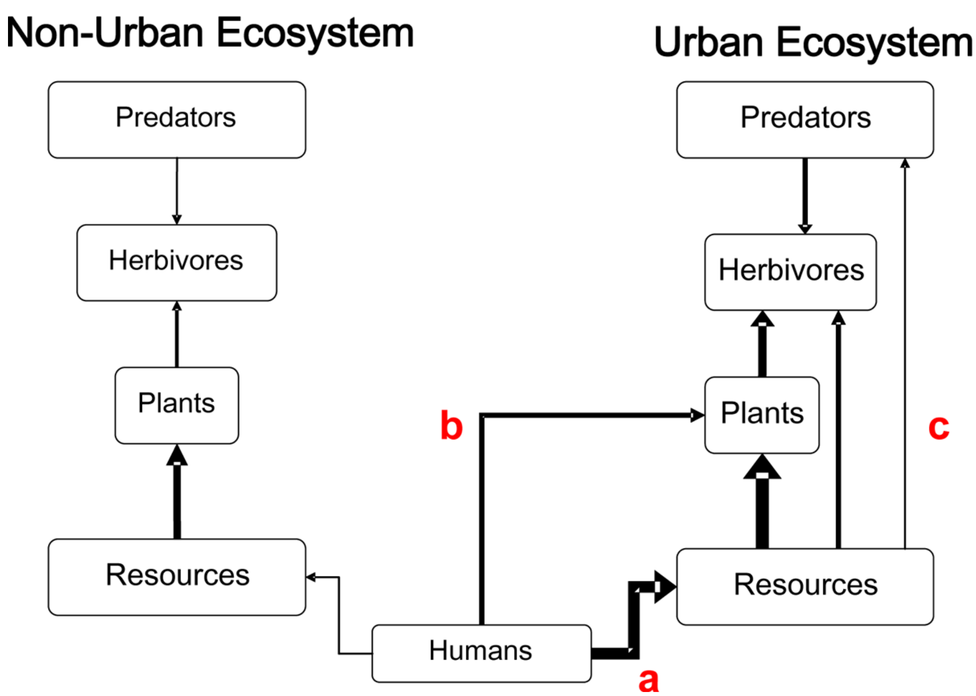

Fig. 1. A generalized model of trophic dynamics in urban vs. non-urban terrestrial systems (modified from Faeth et al. 2005). Humans alter both systems, but in urban environments, human influences are more profound and include (a) enhancement of basal resources like water and fertilizer, and (b) direct control of plant species diversity and primary productivity, leading to strong bottom-up controls. Humans also (c) directly subsidize resources for herbivores and predators either through intentional feeding or unintended consequences of other activities (e.g., garbage, landscape plantings), leading to enhanced top-down control for some taxa and reduced top-down controls on others (see Fig. 2).

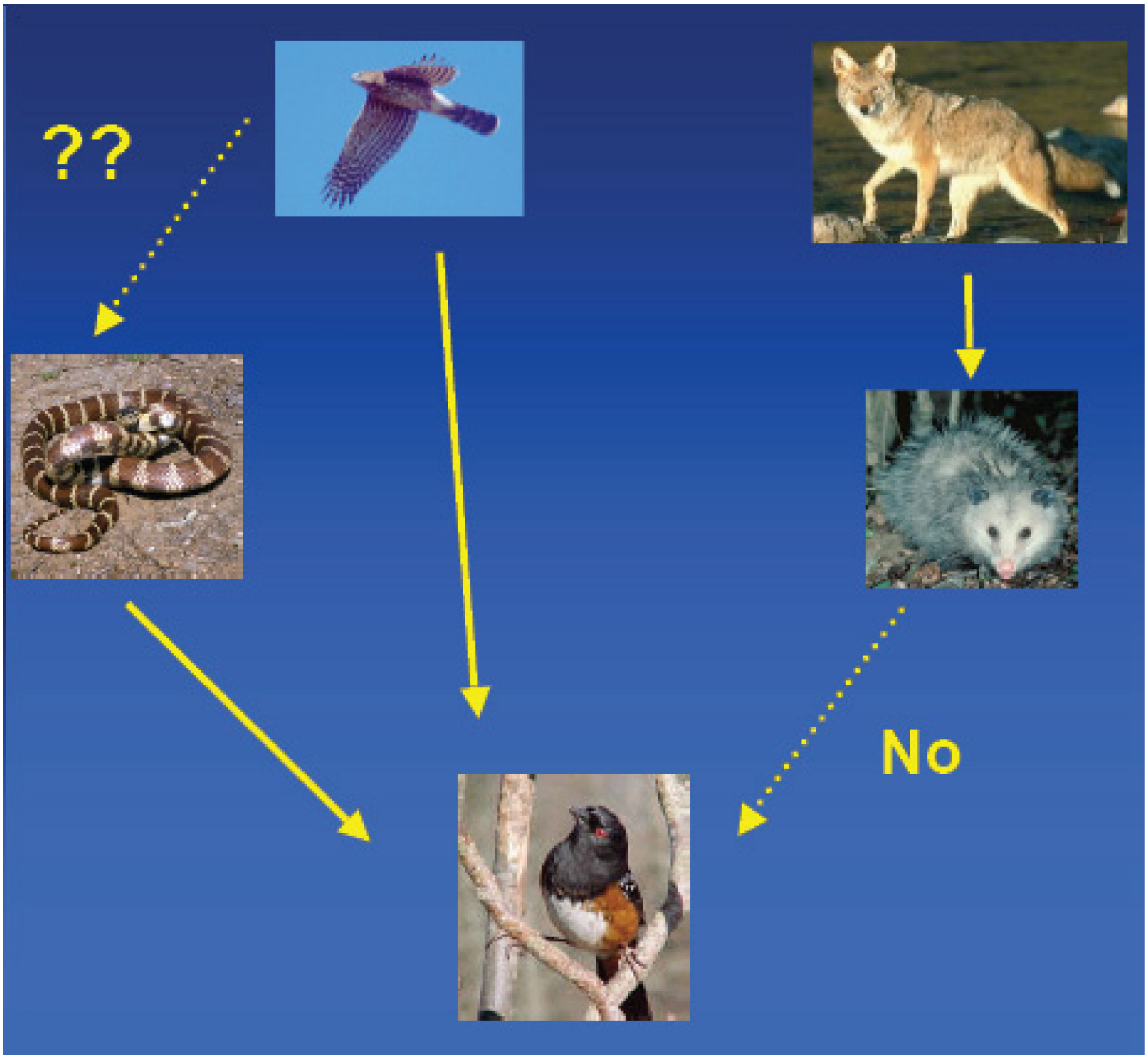

Fig. 2. Putative food web for coastal sage scrub fragments in San Diego, California, from work by Doug Bolger, Jay Diffendorfer, Eric Walters, Michael Anguiano, Dana Morin, and Michael Patten. In smaller, more urbanized fragments raptors increase and snakes decrease, yielding no net change in bird reproductive success. They find a strong connection of raptors and snakes to birds but weak or no connections between mesocarnivores and birds.

countered in any of the pathways of urban food webs, from bottom to top (Fig. 1). Within this system, humans alter and enhance resources and directly influence vegetative biodiversity and primary productivity. Similarly, at higher trophic levels, humans, both directly and indirectly, extirpate some consumers and predators and introduce other, often exotic ones. This fundamental reshaping of the food web in cities leads to altered trophic dynamics, which speakers at the symposium say are often not predictable even with detailed knowledge of species distributions.

Urban systems would appear at first to be driven by bottom-up dynamics, Stanley Faeth stated. His experiments, however, showed that urban arthropod populations on a common native plant species were

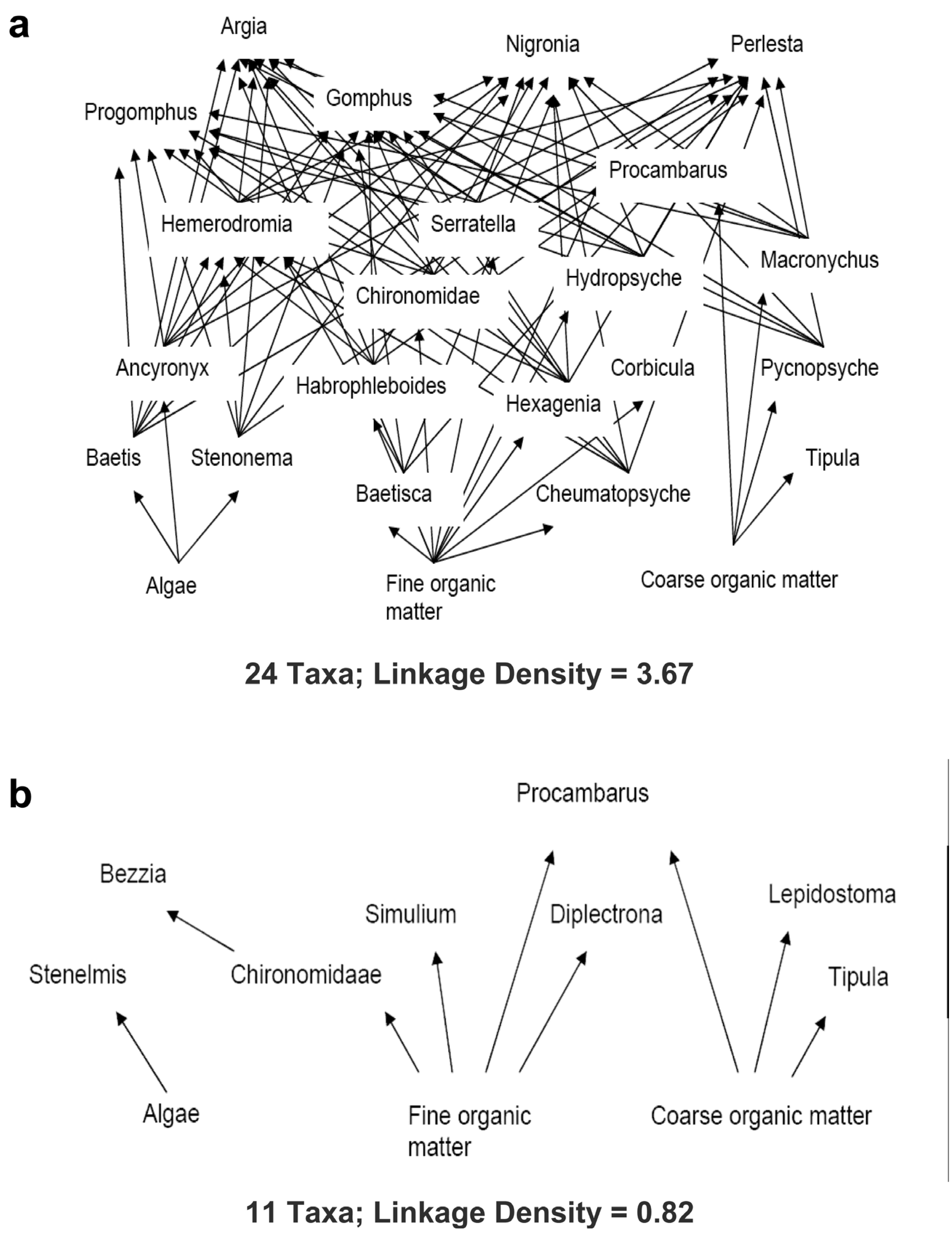

Fig. 3. Putative food webs for (a) Keg Creek, a non-urban reference stream in the Georgia Piedmont, and (b) a stream flowing through a neighborhood in Peachtree City, Georgia, with a mean property value of $388,900. The webs were constructed from data on species occurrence rather than gut content analysis (Overmyer et al. 2005). Species were assigned to functional feeding groups and position in the food web based on information in the literature (J. L. Meyer and S. L. Eggert, *personal communication*).

Fig. 4. Aerial photo of an abandoned village site in the Aleutian Islands region. The enhanced productivity of the village site produces the vivid green area. Rounded dimples within the site are house pits, each marking where a semi-subterranean house once stood. Photo courtesy of Herbert Marschner.

also strongly influenced by top-down control by bird predators, even in unmanaged desert remnant sites. Doug Bolger and his colleagues observed that top-down controls of predator–prey dynamics in San Diego, California, were not the ones that had been previously predicted (Fig. 2). Specifically, avian nesting success in coastal scrub remnants did not decrease with increasing urbanization, as expected. If anything, some birds performed better in the smaller, more urbanized fragments. Other presenters described similar surprises in empirical work ranging from modern cities and suburbs to ancient, abandoned village sites in the remote Aleutian Island region.

Profound influences of humans

To say that humans influence urban food webs is nearly tautological. According to several speakers, however, the profound extent of human influence in urban environments has not yet been fully appreciated by ecologists. Jason Walker showed that plant assemblages in urban sites in Phoenix, Arizona, could not be predicted by any of the factors that affect plant communities in surrounding desert, such as soil nutrients and elevation. Instead, factors such as land use and landscaping design (e.g., mesic vs. xeric) were better predictors of plant assemblages within the urban sys-

Fig. 5. Elevated productivity and human subsidies produced elevated densities of many animal species. In squirrels, high densities lead to low wariness of humans and high levels of aggression. The photo shows squirrels in Lafayette Park, Washington, D.C., where squirrels reach the “highest densities known in the world” according to Tommy Parker, with >40 squirrels/ha.

tem. Judy Meyer noted that in urban streams the effects of human development are consistent enough to identify an “urban stream syndrome.” She found that this syndrome is associated with reductions in food web complexity in urban streams, an effect that appears to be greater in neighborhoods of higher property values (Fig. 3). Covariation in aspects of food web structure and human socioeconomic characteristics was raised by many speakers. Paige Warren and Chris Lepczyk focused on bird feeding by humans, an activity that, as other speakers showed, has broad ramifications throughout the food web. Lepczyk’s landowner survey research showed that the majority of people across a rural-to-urban gradient feed birds, whereas Warren found that neighborhoods vary in the propensity of people to feed birds based on lifestyle characteristics. Furthermore, both Lepczyk and Warren’s surveys found that people intentionally plant vegetation to attract birds and wildlife, including fruit plants, which can both directly and indirectly influence both primary production and consumers. The most striking example of human influence, however, was Nancy Huntly’s work on abandoned village sites in the Aleutian Islands of Alaska. She and her colleagues have found consistent differences in plant and animal diversity and community composition within vs. outside of village sites, differences that have remained stable after >1000 years of abandonment (Fig. 4).

A growing picture of urban food webs

Consistent patterns of human influence emerged in terrestrial systems from the disparate studies presented. Strong bottom-up influences were common across the studies; humans commonly subsidize resources, generating elevated productivity. Eyal Shochat presented evidence that the elevated productivity is associated with higher competition for resources, and ultimately, reduced species diversity, in contemporary urban habitats. In the case of aquatic systems, however, basal resources in urban streams are frequently being impoverished. Predator diversity is often but not always decreased in both terrestrial and aquatic systems, and middle trophic level organisms may experience reduced predation. However, as Doug Bolger and colleagues showed, reticulate food web structure and predator compensation make top-down and bottom-up controls difficult to predict (Fig.2).

Increased population density and altered behavior of urban-adapted animals complicates the effects of shifting productivity and predator communities. Density-dependent behaviors influence predator–prey dynamics, and altered foraging efficiencies may lead to elevated levels of competition. Tommy Parker described the "urban wildlife syndrome," a suite of behavioral characteristics exhibited by many animal species that colonize urban–suburban areas. These characteristics include reduced wariness of humans and increased aggressiveness, both of which are highly density dependent in the gray squirrels he studied (Fig. 5). Human subsidies for squirrels might alter competitive interactions and vulnerabilities to predation. This behavioral syndrome may act as a filter, said Shochat, excluding native species that cannot adapt to the more competitive urban communities. Several questions remain. Does reduced predation risk mediate the decreases in wariness and increases in aggression and foraging efficiency? Or are the altered behaviors simply density-dependent consequences of the increased populations produced by human resources subsidies? Parker noted that several aspects of the urban wildlife syndrome are correlated with resource availability at both habitat and landscape scales. Regardless, it is clear that changes in animal behavior lead to complex responses to altered resource levels.

Differences among studies provide tantalizing questions to be addressed. For example, productivity–diversity relationships differed among the studies, with lower diversity in highly productive habitats within Phoenix and Baltimore, but higher diversity on the highly productive abandoned villages in the Aleutians. Such contradictory findings reflect the broader debate over diversity–productivity relationships in ecology.

Importance of understanding urban food webs

All speakers agreed that altered trophic dynamics in urban environments hold important consequences for conservation of biodiversity, human health, and our broader ecological understanding. Focusing attention on food webs and trophic dynamics can provide insights for conservation biology and environmental management. For example, management to reduce feral cat predation may not have as large an effect as was previously thought on the stability of populations of coastal sage scrub birds (Fig. 2). Furthermore, Meyer noted that urban fishing is an important form of subsistence for many city residents, placing humans squarely within the urban food web. There are immediate human health consequences, she pointed out, for understanding the flow of pollutants through the simplified food webs of urban streams. Finally, Jonathan Chase's concluding remarks laid out opportunities for enhancing basic understanding of trophic dynamics through the study of urban food webs. Topics raised by the speakers, such as predator compensation, diversity–productivity relationships, and effects of predator diversity on food web dynamics, are generally unresolved issues in ecology. Urban environments offer ecologists places where human influences have produced new combinations of species interactions, changes in food web connectivity, and extreme values of productivity, both high and low. The consequences of these alterations are not simple and require an expansion of empirical and theoretical studies to evaluate the impacts and roles of humans in urban food webs.

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