

Invasion, Competition, and Biodiversity Loss in Urban Ecosystems

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Abstract:

The global decline in biodiversity as a result of urbanization remains poorly understood. Whereas habitat destruction accounts for losses at the species level, it may not explain diversity loss at the community level, because urban centers also attract synanthropic species that do not necessarily exist in wildlands. Here we suggest an alternative framework for understanding this phenomenon: the competitive exclusion of native, nonsynanthropic species by invasive species. We use data from two urban centers (Phoenix and Baltimore) and two taxa (birds and spiders) to link diversity loss with reduced community evenness among species in urban communities. This reduction in evenness may be caused by a minority of invasive species dominating the majority of the resources, consequently excluding nonsynanthropic species that could otherwise adapt to urban conditions. We use foraging efficiency as a mechanism to explain the loss of diversity. Thus, to understand the effects of habitat conversion on biodiversity, and to sustain species-rich communities, future research should give more attention to interspecific interactions in urban settings.

Keywords: coexistence | evenness | giving-up density | optimal foraging | rank distribution

Article:

Urban centers are usually characterized by higher animal population densities when compared with wildlands (Emlen 1974, Marzluff 2001, Chace and Walsh 2006, Rodewald and Shustack 2008). Consequently, higher species diversity would be expected in urban areas simply by chance (Connor and McCoy 1979). Instead, urban environments are normally characterized by

lower biodiversity than wildlands (Marzluff 2001, Chace and Walsh 2006). Although the reduction in diversity in urban settings has become a major challenge in conservation ecology (Miller and Hobbs 2004), understanding remains limited of this density-diversity paradox and the mechanisms that lead to the global loss of diversity in urban settings.

Habitat alteration is the major factor ecologists use to explain the loss of diversity (Rosenzweig 1995). Indeed, land-use transformation and changes in vegetation structure are responsible for the extirpation of many native plants and animals from urban settings (Vitousek et al. 1997). However, habitat loss works at the species level. At the community level, although many species may be lost during the urbanization process, the new, constructed habitat will lead to the recruitment of other species. Thus, conversion of one habitat to another may cause a shift in community composition in which some species are lost while others replace them (Grimm et al. 2008). In this case, although community composition may change, there need not be a change in diversity. Data suggest, however, that when urban settings replace deserts, forests, or grasslands, regardless of geographic or climatic zone, species diversity normally decreases (Marzluff 2001, Chace and Walsh 2006). Whereas habitat loss or change is correlated with the pattern of species loss in cities, the processes associated with habitat change that underlie urban species loss are not well studied or understood. Finally, there are very few studies of interspecific competition in urban settings or its affect on diversity (e.g., Petren and Case 1996, Sedlacek et al. 2004).

In this article we explore the role of competition as a driver of urban diversity loss by linking several emerging patterns in urban community ecology. We do not dismiss the role of habitat changes in species extinction and the loss of diversity (e.g., Marzluff 2005), but seek to explain why the number of species gained is generally lower than the number of extirpated species after a new equilibrium is reached following such changes. Our goal is to understand the underlying processes, especially competition, and their role in observed patterns of biodiversity loss in urban habitats.

Recently, Shochat and colleagues (2006) called for the adoption of a more mechanistic approach to urban ecology. Field experiments (Shochat et al. 2004a, Faeth et al. 2005) and modeling exercises (Shochat 2004, Anderies et al. 2007) have emphasized the importance of bottom-up (resource abundance) effects and suggested that species interactions may be important factors shaping urban bird and arthropod communities. Here we take a step forward by suggesting a scenario that may lead to the well-documented global loss of diversity. We hypothesize that urban ecosystems favor a few invasive species that become dominant (both numerically and behaviorally) and out-compete many native, nonsynanthropic species. While the most dominant species in a community may not necessarily be invasive (in most cases nonnative or alien species introduced to the ecosystem by humans) or synanthropic (native species that are highly associated with humans), the association between these two groups in urban settings is very high in most cases. We therefore use these terms alternatively in this article. In the remainder of the article we use population abundance data from two Long Term Ecological Research (LTER)

sites, Phoenix and Baltimore, along with basic ecological theory, to make a case in support of this hypothesis.

Urban bird population regulation

Most cities show gradients of urbanization from the center to the edge along which the influence of biotic and abiotic factors on birds may change. Here we combine both suburban (moderate housing and human density) and urban (high housing and human density) components of the city along this gradient under the term “urban,” and distinguish them from wildland (undeveloped habitats outside of the city). Although suburban areas may differ from urban areas in terms of landscape structure, the intensity of human activities, and bird communities (e.g., increased diversity; Marzluff 2005), both habitats represent constructed environments with similar human activities, resource abundance, and predator abundance that influence top-down and bottom-up controls on urban birds.

Populations are bottom-up controlled if food availability is the limiting factor (Elton 1973, Saunders 1978, White 1978, Schoener 1989), and top-down controlled if predator abundance is the limiting factor (Hairston et al. 1960). Resource and predator densities can also have a combined effect on population size, or change roles at different levels of stress (Menge and Sutherland 1976). As such, higher resource abundance, lower predator abundance, or a combination of both factors may result in higher bird population densities in urban areas than in wildlands.

Despite the difficulties in identifying and quantifying food abundance, food supplementation and stabilization (i.e., reduced seasonal and yearly variation) are the most commonly identified mechanisms for the increase in urban bird population densities (Marzluff 2001). Exotic vegetation, refuse, and bird feeders may all provide food sources for urban birds. Studying northern cardinals (*Cardinalis cardinalis*), Leston and Rodewald (2006) showed that food abundance in urban forests was 2.6 times greater than in rural forests— although, on the basis of bird densities, it is likely that total food abundance was four times greater in the urban habitat (Rodewald and Shustack 2008). Fuller and colleagues (2008) also found a positive correlation between urban bird-feeding stations and bird abundance in Sheffield, Britain.

The role of top-down control, however, is far less clear (Shochat 2004). While many natural predators avoid urban areas, at least during the daytime when birds are active (Tigas et al. 2002), other feral, domestic, or synanthropic predators (e.g., cats, raccoons, and corvids) flourish in urban environments (Haskell et al. 2001). It has therefore been argued that predation pressure in urban settings should be higher than or at least equal to that in wildlands (Haskell et al. 2001, Sorace 2002, Beckerman et al. 2007). Indeed, Baker and colleagues (2005) demonstrated that cat predation could negatively affect dispersal and recruitment of several bird species in urban areas. Experiments with artificial nests also support higher predation rates in urban settings

(Jokimäki and Huhta 2000, Thorington and Bowman 2003), although others have obtained opposite results (Gering and Blair 1999).

In recent years, however, supportive evidence has been gathered for the idea that urban environments are safer for some species than rural habitats and wildlands (Shochat et al. 2006). Predators are known to affect prey at three levels: population size, behavior, and morphology (Kotler et al. 1994, Lima 2002). Most studies on predation in urban settings focused on the population level, as it is easiest to address. Although strong top-down control predicts a negative correlation between predator and prey densities, studies in urban settings consistently indicate that, despite high cat densities, urban bird populations are denser than wildland populations. A recent study on cat and bird populations in the United Kingdom directly indicated that cat and bird densities are positively correlated in urban settings (Sims et al. 2008). Shochat (2004) suggested that urban bird community composition may therefore represent the “ghost of predation past”: Urban environments may have selected a small group of cat-resistant species. These species enjoy high water and food availability and a lack of natural predators, and therefore flourish in the city. Additional and stronger support for this view comes from a study manipulating predator abundance. The removal of black-billed magpies (*Pica pica*) from city parks in Paris demonstrated that these nest predators have a minor effect on both the abundance and reproduction of 14 bird species (Chiron and Julliard 2007). The only obvious effect of magpies appeared to be the shift in foraging niches by some of the remaining species.

The few studies that have addressed behavioral issues further support the low predation-pressure hypothesis. Both birds and squirrels in urban environments demonstrated higher foraging efficiency compared with the wildland habitat (desert and forest, respectively; Bowers and Breland 1996, Shochat et al. 2004a). This possibly indicates that the urban habitat is less risky than the wildlands (Bowers and Breland 1996). In both cases, individuals quit foraging on artificial food patches earlier in wildland or rural habitats than in the urban habitat. While this could be influenced by several factors, the study on urban birds in Phoenix, Arizona (Shochat et al. 2004a), demonstrated that one of the factors is the risk of predation, which is lower in the urban habitat. Birds foraging in urban habitats showed no differences in foraging behavior between food patches that were close to shelters (under bushes) and open patches (Shochat et al. 2004a). In the desert, however, birds depleted resources in areas close to the bush to a greater extent than in those in the open (Shochat et al. 2004a). These findings indicate that birds perceive the city as a safer habitat from predators.

In sum, these findings from recent studies suggest that high bird densities in urban settings are the result of changes in both bottom-up (higher food densities) and top-down (relaxed predation pressure) drivers. These empirical findings serve as the basis for our conceptual framework for addressing species diversity in urban settings.

Evenness, dominance, and changes in species rank distribution

Compared with the straightforward variables of population density and species richness (number of species), evenness, a measure of how individuals are distributed among species in a community, has not been well studied in urban communities. In fact, evenness, which makes up a key component of species diversity, is often overlooked in biodiversity studies (Smith and Wilson 1996). When included in biodiversity studies, it is assumed that communities with higher evenness, when individuals are equally abundant among species in a community, have higher diversity compared with a community with the same number of species but with individuals distributed unequally among species. Urban ecology studies frequently lack quantitative approaches to evenness when comparing urban to wildland community evenness. In Marzluff's (2001) review of urban bird studies, he concluded that evenness decreases in urban settings based on data from 5 out of 9 (56%) studies addressing evenness.

To address and quantify differences in community evenness among land-use types we analyzed species rank distribution data from the two North American LTER urban sites: the Central Arizona-Phoenix (CAP LTER) project, and the Baltimore Ecosystem Study (BES LTER). Our analysis focuses on three habitats: wildlands, agricultural fields, and urban habitat. In many cases, wildlands are first converted to agricultural fields before becoming built environments (Shochat et al. 2004b). With their high resource abundance, agricultural ecosystems differ from many wildlands and resemble urban environments in some ways. In urban environments, the high resource abundance may be a by-product of human activities, whereas in agricultural fields, it is a goal. Regardless, the result is similar: Both ecosystem types are characterized by higher productivity than wildlands. In agricultural fields, however, natural predators that avoid urban habitats may be as abundant as in wildlands (Wu et al. 2006, Koks et al. 2007, Reid et al. 2007). Thus, agricultural ecosystems may represent an intermediate condition between wildlands and urban ecosystems; both historically, through serial land conversion (Shochat et al. 2004b), and ecologically, having top-down effects more similar to wildlands, and bottom-up effects more similar to urban settings.

As discussed above, converting wildlands into urban environments involves changes in both bottom-up and top-down population controls. Past environmental conditions may have selected for traits that enable native species to thrive while preventing potential invasive species from establishing populations or flourishing. Nondrinking animals such as desert rodents, for example, may have an advantage over granivorous birds in extremely dry environments where water is scarce (Shochat et al. 2004a). Once humans remove key hurdles, such as natural predators and lack of food and water, a few invasive species may become more efficient than most nonsynanthropic species in acquiring resources. These can be either endemic synanthropic or alien species with a high level of behavioral plasticity that allows them to adapt quickly to several environmental changes. In either case, such species exploit the changes humans create in the environment. If invasive species are potentially dominant or aggressive, and if they can deplete food patches to a level that does not allow subordinate, native species to acquire food,

then the mechanisms that allow coexistence among species in wildlands could collapse, leading to extinction of less-responsive native species.

If a few invasive or synanthropic species do dominate urban and other human-dominated environments, then we would expect differences in species distribution rank (when all species in the community are sorted from most to least common) between wildland and urban ecosystems. Wildland communities are expected to show a more even profile (the whole spectrum of species distribution rank), with smaller differences in proportions between common and rare species, as illustrated in figure 1. Compared with human-dominated ecosystems (e.g., urban, agricultural), we would also expect to see invasive species replacing nonsynanthropic species at the “top of the chart.” Indeed, when we plot species distribution ranks for spider and bird communities from the CAP LTER, wildland (Sonoran desert) communities appear more even than both agricultural and urban communities. In the desert, spider community structure is relatively even, and total spider abundance is relatively low (figure 2a). Agricultural fields and urban mesic yards exhibit a drastic increase in the total count of individuals and substantial decrease in evenness (figure 2a). Lycosids (wolf spiders), which account for 6% of the individuals in the desert, move from the eighth position to the first position in both agricultural and urban habitats, accounting for 70% and 80% of the whole community, respectively (Shochat et al. 2004b). CAP LTER bird communities show a similar trend, changing from a relatively even desert community to uneven communities in agricultural and urban sites (figure 2b). The house sparrow (*Passer domesticus*) moves from the fifteenth position in the desert, to the fifth in agricultural, to the first position in the residential habitat, with mean abundances of 0.83, 4.78, and 10.77 birds per point count, respectively. Bird communities in the BES LTER wildland (forest) and urban habitats show similar profiles to those in the CAP LTER (figure 2c). Here, the house sparrow moved from the eleventh position in the forest to the first in the urban habitat, followed by European starling (*Sturnus vulgaris*) and rock pigeon (*Columba livia*) in positions two and three. These three alien species accounted for 51% of the entire urban bird community in Baltimore.

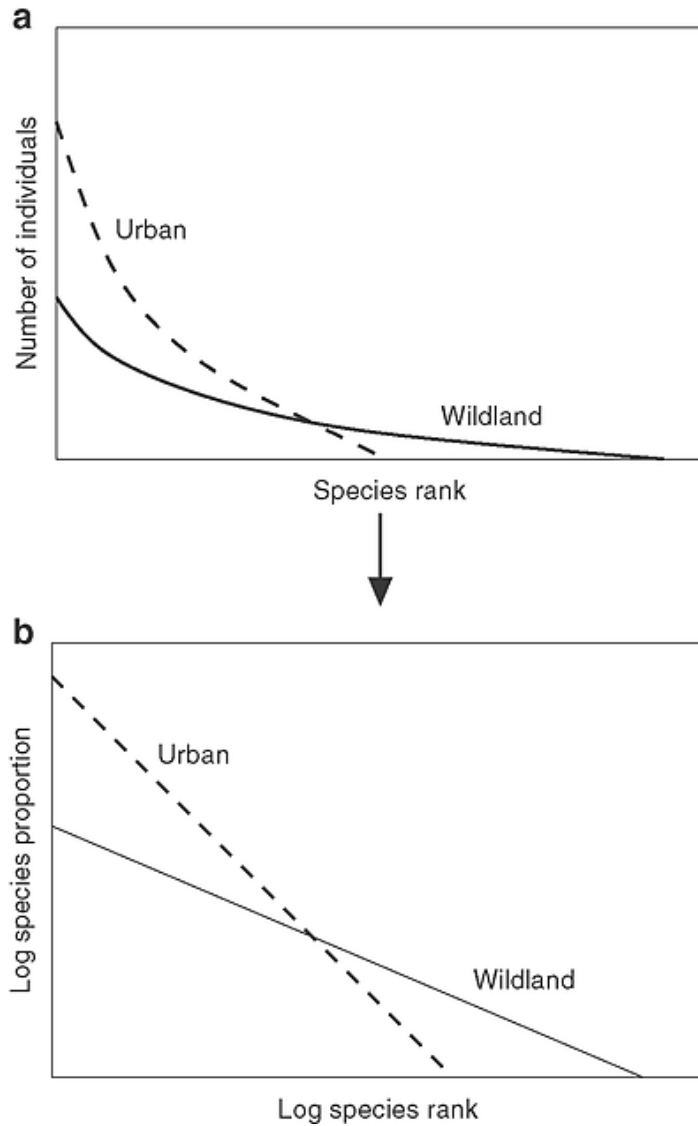


Figure 1. (a) Predicted differences in evenness between wildland and urban habitats. Urban communities are expected to be less even, with the most common species accounting for a higher proportion of the whole community. These synanthropic species also out-compete native species, resulting in lower species richness than in wildlands. (b) Log transformation of species rank and proportion are predicted to mimic linear lines with negative slopes that are steeper for urban communities than for wildland communities.

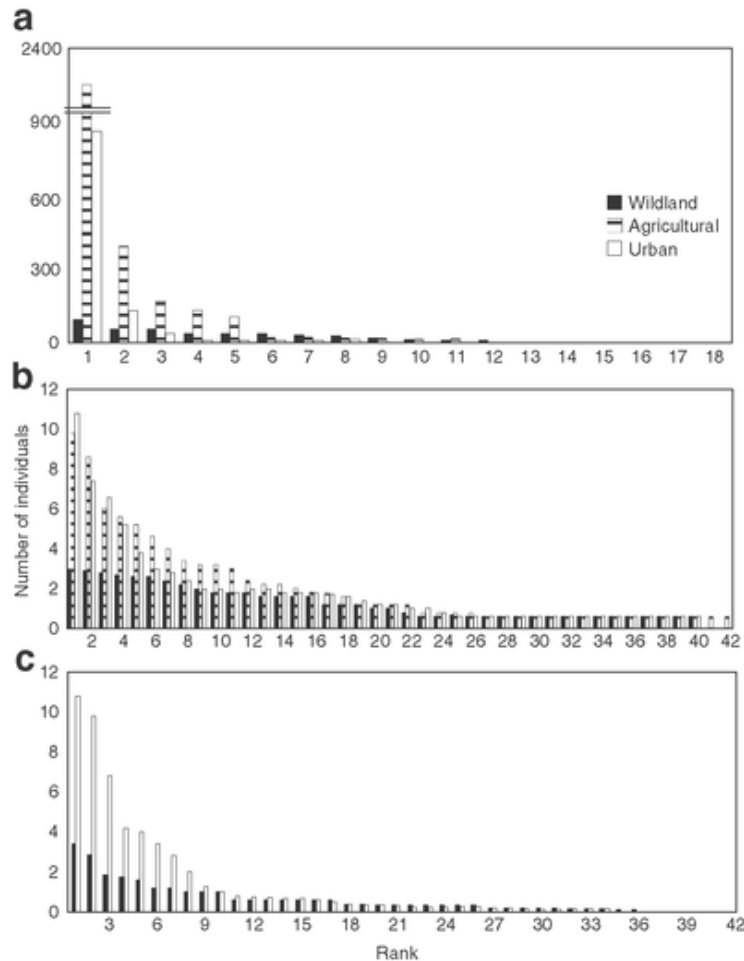


Figure 2. Community profiles. Species rank distribution patterns from three projects of the two North American Long Term Ecological Research (LTER) urban sites: the Central Arizona-Phoenix (CAP LTER) project and the Baltimore Ecosystem Study (BES LTER). The number of individuals versus rank of (a) CAP LTER spider families, (b) CAP LTER bird species (spring 2004), and (c) BES LTER bird species (spring 2005). “Wildland” is represented by Sonoran desert in CAP LTER and deciduous forest in BES LTER. For census methodology, see Shochat and colleagues (2004b) and Kinzig and colleagues (2005).

Log transformations of these relationships tend to generate linear functions, which make species rank distributions easier to compare. The less even a community, the steeper its negative slope. An analysis of covariance (ANCOVA) test with a post-hoc test (Tukey B) shows that the differences in species rank distribution between wildlands and urban habitats are significant in all three cases. In the CAP LTER project, agricultural and urban habitats show steeper negative slopes than desert for both spider families (ANCOVA, $F_{1,2} = 42.785$, $P < 0.001$) and bird species (ANCOVA, $F_{1,2} = 38.730$, $P < 0.001$). For bird communities in the BES LTER, the urban habitat shows a steeper negative slope than the forest (ANCOVA, $F_{1,1} = 51.521$, $P < 0.001$). Finally, in all three cases, wildlands are richer in diversity than urban habitats (figure 3).

Interestingly, in CAP LTER, agricultural habitats retain a high level of diversity, similar to the Sonoran desert, despite the change in community profile (figure 3a, 3b).

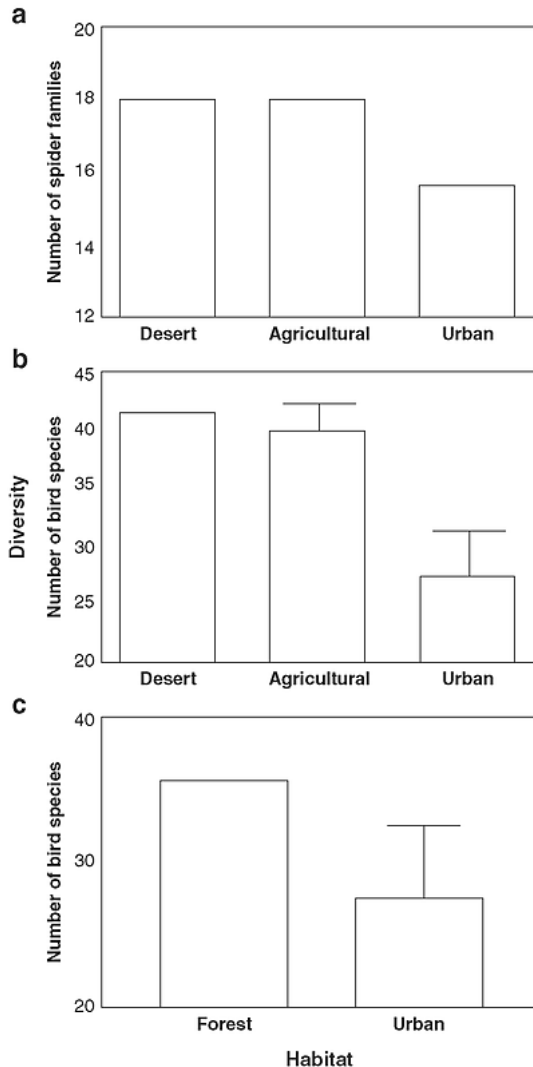


Figure 3. Biological diversity in wildland, agricultural and urban habitats. In the Central Arizona-Phoenix (CAP LTER) project, the agricultural habitat retains spider (a) and bird (b) communities that are as rich as in the Sonoran desert, but biological richness declines in the urban habitat (rarefaction, $P < 0.01$). In the Baltimore Ecosystem Study (BES LTER), bird (c) species diversity in urban parks is lower than in forest patches (rarefaction, $P < 0.01$). Error bars are given where rarefaction was used to control for sample size (CAP LTER and BES LTER bird census data).

How are the patterns of community profile and diversity associated? We suggest that the decrease in evenness and the dramatic change in community profile is a key pattern for assessing the complex process of diversity loss. The population size of synanthropic species remains restricted in wildlands because of limited resource abundance and, possibly, a high density of

natural predators. As long as these populations cannot grow beyond a particular threshold, less-responsive species can coexist with, and even dominate, synanthropic species in wildlands. In urban environments, however, changes in the bottom-up (higher productivity and predictability of resource input) and, to a lesser degree, top-down drivers (lower predation pressure) set new rules for the ecological and evolutionary game (Shochat et al. 2006). We suggest that both factors, especially the bottom-up effect, favor a few synanthropic species. Such species thrive, dominate the community, and utilize most of the available energy, leaving fewer resources for their competitors. In the long term, the competition for resources may cause local extinction of potentially adaptable native species (species that can find a suitable habitat in urban settings), leading to reduced biodiversity, a pattern recognized worldwide (Marzluff 2001, Chace and Walsh 2006, Grimm et al. 2008).

How plausible is this scenario? Studies on optimal foraging in urban settings (Shochat et al. 2004a) suggest a mechanism that may lead to changes in community structure and eventually loss of diversity.

A potential mechanism for the collapse of coexistence

Giving-up densities (GUDs), the amount of food remaining on artificial food patches (trays of seed mixed in sand, in our case), reliably measure foraging efficiency (Brown 1989). Lower GUDs indicate greater foraging efficiencies, because they are based on diminishing returns: As food density in the patch decreases, it becomes increasingly difficult to find the next food item. Thus, very efficient species can still find food in patches of low resources, where less-efficient species have already quit. For that matter, forager density is not expected to influence the GUD, because despite minor differences between individuals, the species morphology—combined with other local factors influencing the costs and benefits of foraging—will determine the “quitting harvest rate” (Brown 1988), an equivalent for the GUD.

In a set of field experiments, Shochat and colleagues (2004a) have shown that bird foraging efficiency was higher in urban settings than in desert habitats. A recalculation of GUD from this CAP LTER project for all species with large enough sample size (the four most common species in each habitat) is presented in figure 4a. Sorted by increasing efficiency, urban species have significantly lower GUDs than desert species (pairwise comparison, $t = 4.09$, $N = 4$, $P = 0.026$). In other words, the most common bird species in the urban habitat are more efficient foragers than those in the desert. Regardless of whether these differences in GUD indicate (a) changes in predation risk, or (b) differences in species foraging abilities on the basis of their morphology, the results still indicate that urban species can exploit larger amounts of food from a given patch.

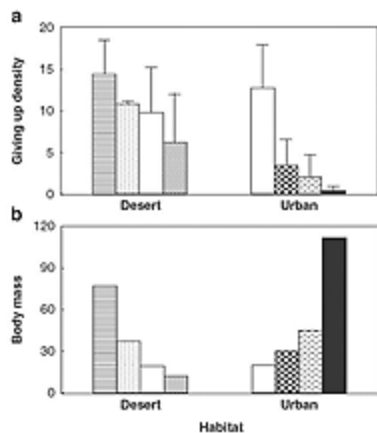


Figure 4. (a) Giving-up densities (GUD) and (b) body mass (in grams) of bird species that visited seed trays in the greater Phoenix area. Error bars represent mean GUD for each species. Of the seven species with large sample sizes, only the house finch (empty bars) was found in both urban and desert habitats. Curve-billed thrasher (horizontal stripes), cactus wren (dots), and black-throated sparrow (diagonal stripes) were found in the desert; house sparrow (checkered), Inca dove (dashed stripes), and mourning dove (black) were found in urban habitats. For methodology, see Shochat and colleagues (2004b).

The key to understanding the cause for diversity loss and unevenness is suggested in figure 4b. There is a negative correlation between body mass and GUD in the desert. In the urban habitat, this correlation is positive. Because dominant species are normally characterized by higher body mass than subordinate species (Schoener 1989, Poling and Hayslette 2006), this pattern may explain a failure of the mechanism of coexistence, as explained below. Over the long term, this failure must lead to local extinction and loss of diversity.

Because the food used in this experiment was millet, our optimal foraging results should be interpreted with care. The two most dominant species in the desert were omnivores, not specialist granivores, so the overall higher GUDs in the desert (figure 4a) are expected. The dominant desert species are inefficient foragers because they do not specialize in seed consumption, but this does not pose a problem for explaining community structure. Actually, this dominant species behavior explains the mechanism that allows for the existence of a more balanced bird community in the desert than in the urban community. Whereas these two dominant native species in the desert leave high enough densities of food in a given patch for the subordinate ones, the dominant urban species—Inca dove (*Scardafella inca*) and mourning dove (*Zenaida macroura*; figure 4b)—are obligatory granivores, and are the most efficient foragers in the community. Thus, an important mechanism of coexistence, temporal partitioning, whereby the subordinate species are the most efficient foragers and therefore can deplete food patches after the dominant species quit (Ziv et al. 1993), fails to work in urban settings. A failure of this

coexistence mechanism should lead to exclusion of subordinate species from the community and a loss of diversity in the long term.

It is important to note that the two most common species visiting desert seed trays, curve-billed thrashers (*Toxostoma curvirostre*) and cactus wrens (*Campylorhynchus brunneicapillus*), are common in urban habitats in Phoenix. Additionally, white-winged doves (*Zenaida asiatica*) and mourning doves are also present in large numbers in the Sonoran desert, but, because birds may shift their diet in different habitats (e.g., Sauter et al. 2006), these species rarely visited seed trays in these habitats (Shochat et al. 2004a). Yet from the subordinate species' point of view (in this case, any small granivore species), the question is: What is the dominant species with which it competes? In the urban habitat the dominant species are doves, which are highly efficient granivores, setting a coexistence challenge that may be too difficult for at least some of the small seedeaters. Why are dove species less efficient granivores in the desert than in the urban habitat? The reason may be that many bird species specialize in different food sources in different habitats. By shifting from one source to another in a given habitat, dominant species may open or close a niche to subordinate species. For example, white-winged doves appear to forage mostly on saguaro fruit in the Sonoran desert. This species was not observed foraging on our seed trays, possibly because its “search image” for food differs between urban and desert habitats. Since saguaros are far less common in the urban habitat, white-winged doves have to shift their diet. If urban settings force the white-winged dove to shift from frugivory to granivory, its high efficiency of seed depletion may exclude from the urban habitat small granivore species that can coexist with the dove in the desert. Future research on species coexistence may benefit from assessing whether diet shift is a more general phenomenon, and from learning its role in species coexistence.

Specific examples of urban winners and losers

It is very difficult to address which species are likely to be missing from an ecosystem as a result of competitive exclusion (or any other reason). Large-scale (both space and time) experiments to specifically address this question may be almost impossible to carry out. Our general point is that where one family accounts for 80% of the overall community, as is the case with the lycosids in the CAP urban habitat, there are naturally far fewer resources left for the rest.

In both study sites (BES and CAP), the house sparrow, an aggressive and fairly efficient forager, became the most abundant species in the urban habitat. In the CAP, current experiments that test competition for food between house sparrows and lesser goldfinches (*Carduelis psaltria*) on feeders by excluding the former indicate that house sparrows directly affect behavior and abundance of the lesser goldfinch within the scale of an individual backyard. Given perfect foraging conditions, house sparrow density increases, causing a decrease in goldfinch abundance, and, in extreme cases, leading to “local extinction.” The presence of the lesser goldfinch in the urban habitat must be the result of this species' ability to explore other foraging opportunities or patches not explored by the house sparrow, but the ability of the house sparrow to affect its

numbers drastically may suggest that many other small granivores may fail to establish in the greater Phoenix area owing to competition. One of these species may be the black-throated sparrow (*Amphispiza bilineata*), which is occasionally seen in suburban areas (although not established, suggesting that the habitat may be suitable), but remains restricted to the desert in central Arizona. This species has a lower body mass but appears to be a less-efficient forager than the house sparrow (figure 4). The black-throated sparrow is widespread throughout the southwestern United States, but is missing from urban habitats. It is possible that lower immigration rates compared with extinction rates prevent its establishment in urban habitats in central Arizona. The negative effects of the house sparrow on smaller granivorous species demonstrate how exclusion at a small scale (“backyard competition”) may add up to exclusion at the larger scale (the urban habitat).

Whereas many invasive synanthropic species are likely to negatively influence nonsynanthropic birds that have not coevolved with them, they should not be expected a priori to do so. It is possible that some invasive species manage to invade relatively unoccupied niches and have minor effects on the local avifauna. Koenig (2003) argued against the idea that the European starling is out-competing local cavity-nesting species in North America. Using meta-analysis he demonstrated that of 24 species of cavity nesters, only 4 were likely to be affected by the presence of starlings. Blewett and Marzluff (2005) supported this idea in Seattle. Although not studied in CAP, the situation appears to be similar. Whereas European starlings breed in many holes in cavities drilled by gila woodpeckers (*Melanerpes uropygialis*) in trees and saguaros, the gila woodpecker thrives in the urban part of the greater Phoenix area. Altogether, the effect of invasive species on urban bird community structure requires detailed, species-based studies to understand which of the species are likely to cause reduction in species diversity through aggressive competition.

Future directions

In search of a common mechanism for the global loss of diversity in urban settings, we have combined patterns from community evenness studies and findings from optimal foraging field experiments. Figure 5 summarizes the scenario that leads from an even wildland community to an urban community with a few, dominant winner species and many loser species, a process mediated by human activities.

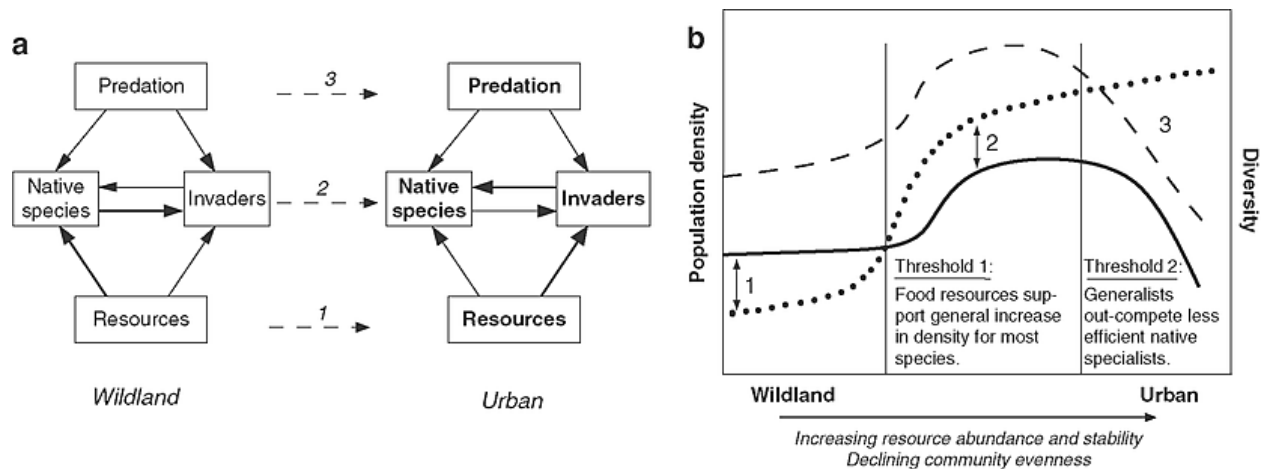


Figure 5. (a) Processes of urban bird communities. (1) Food resource abundance increases with urbanization, supporting higher overall bird densities. Introduction of human-provided foods supports greater numbers of invader species than nonsynanthropic species. In wildlands, the greater variety of specialized food resources are captured more efficiently by nonsynanthropic species. (2) Competition between nonsynanthropic and invader, synanthropic species, corresponds to species composition, resource availability and predator communities. Invaders become more dominant over nonsynanthropic species in urban areas. (3) Predation mediates competition between species in wildlands, but becomes less important in urban areas. (b) Patterns of urban bird communities. Changes in population densities (solid and dotted lines) and species diversity (dashed line) along the wildland-urban gradient. (1) In wildlands, nonsynanthropic species (solid line) out-compete invaders (dotted line). (2) At intermediate levels of urbanization, both groups of species are still present. Invasive species increase in density more rapidly than nonsynanthropic species by exploiting novel, stable, and homogenized food resources (e.g., commercial seed mixture). Nonsynanthropic species persist through spatial partitioning, exploiting remnant patches with specialized food or other resources. Potential for longer-term declines in nonsynanthropic species. (3) At high levels of urbanization, coexistence mechanisms collapse. Predation pressure is relaxed. Food resources are relatively homogenous in distribution and quality, and are many times more abundant than in wildlands. Invasive species become dominant foragers rather than subordinate. Nonsynanthropic specialist species become locally extinct.

The loss of diversity in urban environments is a global phenomenon for many animal taxa. The lack of a serious effort to understand the mechanisms underlying this pattern is therefore puzzling. In order to create a theoretical framework for the loss of diversity, Marzluff (2005) developed and tested a model based on the island biogeography concept (MacArthur and Wilson 1967). Bird diversity in Seattle peaked at intermediate levels of urbanization, where the proportion of forest was still relatively high. The high species richness in this part of the landscape resulted from a great increase in richness of early successional birds (species that are found in a variety of habitats around the area). Extinction rates of forest species and immigration

rates of synanthropic species played a minor role influencing species diversity. As the built environment became increasingly dominant in the landscape, the loss of forest species exceeded the immigration and establishment rates of synanthropic species. Marzluff (2005) therefore suggested that the overall sum of bird species should be lower in the most urbanized parts of the landscape. This study may represent the only mechanistic approach to species diversity loss in urban environments to date.

Whereas Marzluff (2005) suggested a mechanism that is based largely on habitat selection, our suggested mechanism emphasizes species interactions. Invasive species, in most cases alien species, are recognized as one of the biggest threats to species diversity (Wilcove et al. 1998), and many of the most common urban species around the world are invasive (e.g., rock pigeon, house sparrow, common mynah [*Acridotheres tristis*]; Shochat et al. 2006). Thus, extinction as a result interspecific interactions in urban settings is likely to add to the negative effects of habitat loss or habitat compromises for many native, nonsynanthropic species. We therefore do not suggest favoring one approach over the other, but rather suggest focusing on the role of both habitat and competition in diversity loss in urban environments.

Invasive species have negative effects on local diversity, either by causing niche shifts or local extinctions (Mooney and Cleland 2001). Furthermore, the out-competition of a native species by an invasive species can be the result of competition for food per se, as shown for squirrels in Britain (Kenward and Holm 1993). Our work addresses the population level and emphasizes the “missing link” between the individual level (foraging behavior) and the community level (species diversity). Future research should test whether extreme increase in resource abundance leads to loss of diversity in the long term, how population densities change, and whether it leads to the predicted change in community profile (figure 1).

Our results suggest that intermediate environments between urban and wildland habitats may help assess the processes that lead to the reduction in diversity. Agricultural habitat communities show mixed characteristics between wildland and urban landscapes, and may therefore help refine our understanding of the competitive-interaction mechanism that we propose. Whereas the high productivity of agrarian habitats changes community composition and decreases evenness (figure 2), these communities retain high biodiversity (figure 3). This suggests that while an increase in productivity per se brings invasive species to a “better position” in the community, further changes in ecological conditions may be required to allow them to exclude nonsynanthropic species. Although this finding does not fully support our hypothesis that increased productivity should eventually cause the loss of diversity, changes in habitat structure may be an even less likely mechanism because it would predict loss of diversity when wildlands are converted to agricultural fields. Thus, despite differences in habitat structure, future research should address which features are similar between wildlands and agricultural habitats and the ways these features differ in urban habitats.

On the basis of empirical results from field experiments on optimal foraging in safe versus risky microhabitats (Shochat et al. 2004a), it is possible that altered predation pressure in urban environments provides the additional opportunities for synanthropic species to out-compete desert species. If predation pressure in agricultural habitats remains as high as it is in wildlands (Bowers and Breland 1996), but decreases in urban environments, it may help maintain high diversity in agroecosystems through the well-established mechanism of predator-mediated species coexistence (e.g., Bouskila 1995, Brown and Kotler 2004). High predation pressure may therefore add to the low resource abundance in keeping the carrying capacity of wildlands low for potential invasive species. Although overall results suggest that the observed inequality in urban ecosystems is primarily caused by increased habitat productivity associated with human activities, future research should aim to tease apart bottom-up and top-down effects in urban ecosystems, including agricultural environments.

Understanding the mechanisms that allow invasive species to become more abundant is the first step in conservation and reconciliation ecology (Rosenzweig 2003). Although a full control of population size is impossible for many of these species, a partial control may help to keep populations of invasive species low enough to open niches for subordinate species. Squirrel-proof feeders are good examples of a possible solution. Whereas they do not have an obvious negative effect on squirrel population, use of the feeders reduces pressure on urban bird species simply by giving them better access to food resources. Current field experiments from the CAP LTER indicate that similar results can be achieved by designing a sparrow-proof seed feeder, to support higher population densities of the subordinate lesser goldfinch in the urban environment.

Future studies designed to address top-down and bottom-up controls on species richness may shed additional light on the linkages among habitat productivity, predation pressure, community evenness, and species diversity loss in agricultural and urban settings, and determine whether dominance slopes (figure 1b) that lie within particular ranges of values can characterize different ecosystems or taxa. If top-down or bottom-up controls on synanthropic species contribute to these species' ability to out-compete other species, then understanding these processes will be an important step in restoring diversity and promoting environmental sustainability in human-dominated environments.

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