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Urbanization, Biodiversity, and Conservation

MICHAEL L. MCKINNEY

Among the many human activities that cause habitat loss (Czech et al. 2000), urban development produces some of the greatest local extinction rates and frequently eliminates the large majority of native species (Vale and Vale 1976, Luniak 1994, Kowarik 1995, Marzluff 2001). Also, urbanization is often more lasting than other types of habitat loss. Throughout much of New England, for example, ecological succession is restoring forest habitat lost from farming and logging, whereas most urbanized areas in that region not only persist but continue to expand and threaten other local ecosystems (Stein et al. 2000).

Another great conservation challenge of urban growth is that it replaces the native species that are lost with widespread “weedy” nonnative species. This replacement constitutes the process of biotic homogenization that threatens to reduce the biological uniqueness of local ecosystems (Blair 2001). Urban-gradient studies show that, for many taxa, for example, plants (Kowarik 1995) and birds and butterflies (Blair and Launer 1997), the number of nonnative species increases toward centers of urbanization, while the number of native species decreases.

The final conservation challenge of sprawl is its current and growing geographical extent (Benfield et al. 1999). A review by Czech and colleagues (2000) finds that urbanization endangers more species and is more geographically ubiquitous in the mainland United States than any other human activity. Species threatened by urbanization also tend to be threatened by agriculture, recreation, roads, and many other human impacts, emphasizing the uniquely far-reaching transformations that accompany urban sprawl.

About 50% of the US population lives in the suburbs, with another 30% living in cities (USCB 2001). Over 5% of the total surface area of the United States is covered by urban and other built-up areas (USCB 2001). This is more land than is covered by the combined total of national and state parks and areas preserved by the Nature Conservancy. More ominously, the growth rate of urban land use is accelerating faster than land preserved as parks or conservation areas by the Conservancy (figure 1). Much of this growth is from the

THE IMPACTS OF URBANIZATION ON NATIVE SPECIES ARE POORLY STUDIED, BUT EDUCATING A HIGHLY URBANIZED HUMAN POPULATION ABOUT THESE IMPACTS CAN GREATLY IMPROVE SPECIES CONSERVATION IN ALL ECOSYSTEMS

spread of suburban housing. It is estimated, for example, that residential yards occupy 135,000 acres in the state of Missouri (MDC 2002). This residential landscape represents nearly 1% of the total area of Missouri and is nearly three times the area occupied by Missouri state parks.

Here I review the growing literature that documents how urban (and suburban) expansion harms native ecosystems. This knowledge can aid conservation efforts in two major ways. One is through the use of ecological principles—such as preserving remnant natural habitat and restoring modified habitats to promote native species conservation—to reduce the impacts of urbanization on native ecosystems. Rare and endangered species sometimes occur in urbanized habitats (Kendle and Forbes 1997, Godefroid 2001) and thus could be conserved there. Managing the large amount of residential vegetation (1% of the state area, as noted above) in ways that promote native plants and animals could also make a significant contribution to conservation.

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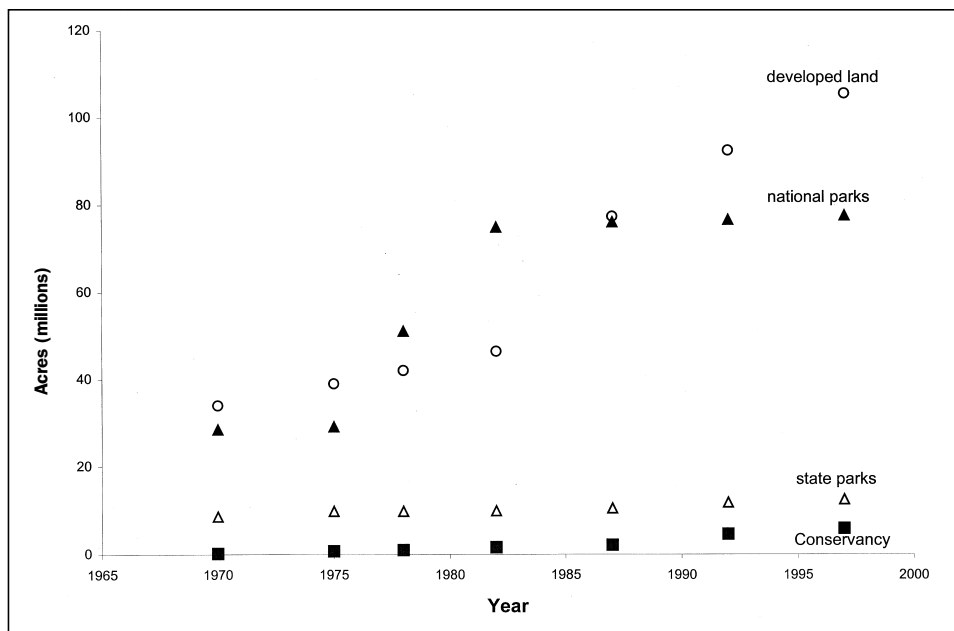


Figure 1. Amount of land covered in the lower 48 states, by category. Source: All data are from Statistical Abstract of the United States for the years shown, except for Nature Conservancy data, which is from Stein and colleagues (2000).

A second way in which the study of urban ecology can serve conservation is by helping to develop a more ecologically informed public. Providing a well-informed public could be the most important application of urban ecology, as a means of promoting effective conservation of native species (Kendle and Forbes 1997). Because 80% of the American public lives in or near urban areas, there are many opportunities for creating an informed public that can wield enormous economic and political pressure to promote conservation policies. People who live in urban environments often have a great appreciation of many urban species, such as birds (Clergeau et al. 2001). Indeed, residents of suburban and urban areas tend to place a much higher value on species conservation than those living in rural areas (Kellert 1996). This is reflected in voting behavior: Legislators from highly urbanized states and districts tend to be more supportive of strengthening the Endangered Species Act (Mehmood and Zhang 2001).

Unfortunately, these conservation opportunities are hindered by the very poor ecological knowledge of typical American urbanites. A survey of Texas high school students, for example, showed that 60% of the students misidentified the opossum as a rodent and that ecological understanding of human effects on biota was even poorer; only 2% of the students knew that raccoons tend to benefit from many human activities (Adams et al. 1987).

The urban–rural gradient: General patterns

Urban-to-rural gradient studies examine changes in plants and animals along a transect from the inner city to surrounding, less-altered ecosystems; they also show what happens to sur-

rounding native ecosystems as urban sprawl expands. General patterns that emerge from these studies are described below.

Physical gradients. Physical changes along the gradient strongly influence available habitat for native species. A number of reviews (Sukopp and Werner 1982, Medley et al. 1995, Pickett et al. 2001) show increases in these physical changes, as one moves toward the urban core, in such metrics as human population density, road density, air and soil pollution, average ambient temperature (“heat island” effect), average annual rainfall, soil compaction, soil alkalinity, and other indicators of anthropogenic disturbance. The percentage of area that is impervious surface (pavement, asphalt, buildings) ranges from well over 50% at the

urban core to less than 20% at the fringe of urban expansion (figure 2). In addition, the amount of subsidized energy and matter imported for use by humans and available to other species increases toward the urban center (Collins et al. 2000, Pickett et al. 2001).

Habitat-loss gradient. These physical changes produce a gradient of natural habitat loss that steepens from rural areas toward the urban center. As habitat is lost, it becomes increasingly fragmented into more numerous but smaller remnant patches (Medley et al. 1995, Collins et al. 2000). The lost natural habitat is then replaced by four types of altered habitat that become progressively more common toward the urban core. The four types of replacement habitat are listed below, in order of increasing habitability to most native species and decreasing proportion of coverage toward the urban core. The latter three types are based on Whitney (1985).

1. Built habitat: buildings and sealed surfaces, such as roads
2. Managed vegetation: residential, commercial, and other regularly maintained green spaces
3. Ruderal vegetation: empty lots, abandoned farmland, and other green space that is cleared but not managed
4. Natural remnant vegetation: remaining islands of original vegetation (usually subject to substantial nonnative plant invasion)

Diversity changes along the urban–rural gradient

It is probably intuitive to even the most casual observer that the increasing fragmentation of natural habitat by human disturbances in the direction toward urban centers will tend to reduce species richness (number of species) in that direction. There are, however, many variables that can affect the rate and consistency of species loss along the gradient, so empirical studies are crucial in measuring urban impacts.

Urban core, low diversity.

Many studies document that the lowest species diversities along the urban–rural gradient occur in the intensively “built” environments of the urban core. This has been shown for many taxa, including plants (Kowarik 1995), birds and butterflies (Blair 2001), many insects (Denys and Schmidt 1998, McIntyre 2000), and mammals (Mackin-Rogalska et al. 1988). In all these taxa, the number of species at the urban core is reduced to less than half of that found in the rural, more natural areas at the opposite end of the gradient (figure 2).

Blair (2001), for example, found just 7 summer resident bird species in the central business district of Palo Alto, California, compared with 21 species that inhabited a natural area (preserve) outside the city limits. Similar reductions were found for birds and butterflies in other cities, as shown by Blair’s (2001), and especially by Marzluff’s (2001), comprehensive compilation of studies on urbanization impacts on birds.

Much of the reduction in richness is obviously caused by the loss of vegetation. The number of species of animal taxa, such as birds (Shugart et al. 1975) and insects (Majer 1997), tends to correlate with the number of plants in an area. Also, area covered by vegetation is a good predictor of species numbers for birds (Goldstein et al. 1986); mammals, amphibians, and reptiles (Dickman 1987); and insects (McIntyre 2000).

As over 80% of most central urban areas is covered by pavement and buildings (Sukopp and Werner 1982, Blair and Launer 1997), less than 20%, therefore, remains as vegetated area. Furthermore, the remaining vegetated habitat often contains low plant diversity as a result of erosion, trampling, pollution, invasion or cultivation of a few nonnative species, and many other human disturbances. Also, mowing, prun-

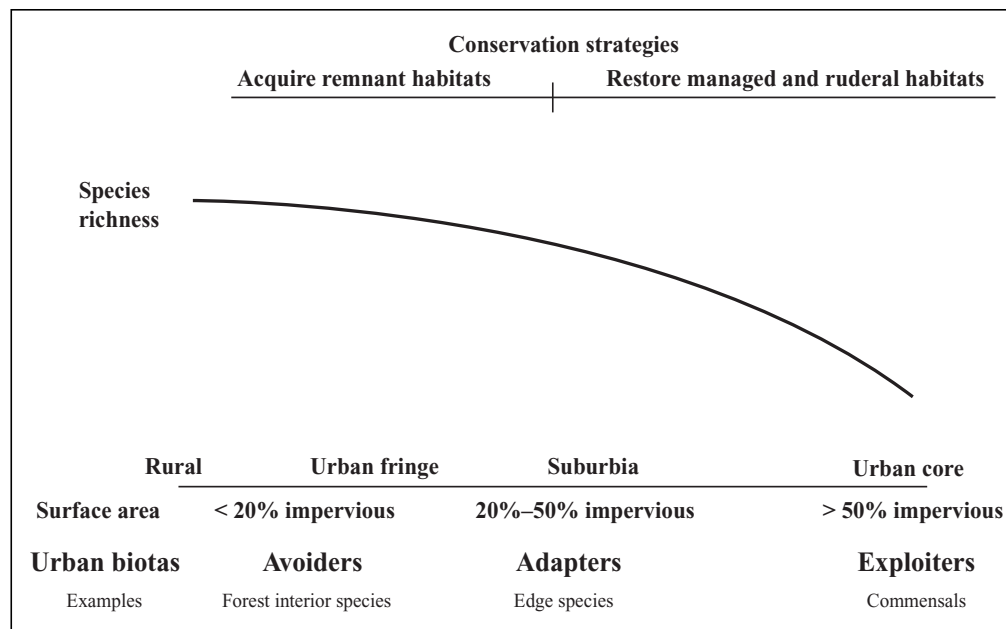


Figure 2. Urban–rural gradient. This is a very generalized and simplified depiction of changes in surface area, species richness, and composition, as compiled from a number of sources discussed in the text. Two basic conservation strategies with respect to urban sprawl are shown at the top.

ing, and other common landscaping practices further reduce the volume of the remaining vegetation (Gilbert 1989, Adams 1994).

Suburban diversity: Peak or plunge? Some studies indicate that species richness tends to be higher in areas with low to moderate levels of human development (such as outlying suburban developments) than in more natural rural areas such as preserves. This suburban peak in species numbers is evident in many taxa, such as mammals (Racey and Euler 1982), birds and butterflies (Blair 2001), bumblebees (Pawlikowski and Pokorniecka 1990), ants (Nuhn and Wright 1979), lizards (Germaine and Wakeling 2000), and plants (Kowarik 1995).

An explanation often suggested for this suburban peak (e.g., Blair and Launer 1997, Germaine and Wakeling 2000, Blair 2001) is the intermediate disturbance hypothesis. The initial human impacts of suburban sprawl are sometimes relatively mild, with only a few housing subdivisions in a matrix of largely natural or agricultural habitat. This promotes environmental heterogeneity, because different habitats occur alongside one another. Such habitat diversity is enhanced by the fact that individual homeowners often make individualistic choices in the plants that they cultivate (Henderson et al. 1998).

In addition to providing spatial heterogeneity, these anthropogenic habitats are typically very productive (Falk 1976), being highly subsidized in scarce resources, ranging from water to nutrients (e.g., fertilizers). Cultivated plants include many ornamentals that often bear fruits and seeds that are uti-

lized by animals, especially birds and bats (Munyenembe et al. 1989, Adams 1994). Some animals have adapted to the direct consumption of human resources (Adams 1994) that are provided accidentally (garbage) or intentionally (bird food).

In contrast to the above, other studies show that suburban areas have reduced species diversity compared to less-altered rural habitats (figure 2). For example, Marzluff's (2001) compilation of 51 bird studies found that 31 of the studies (61%) showed lower species richness in suburban and other areas of human settlement, compared with more natural rural areas. The remaining 20 studies reported either an increase or no change in diversity with increasing human settlement. The 51 studies covered a wide range of geographic and natural settings, so it is difficult to identify which variables determine whether a rise or fall of species richness occurs with increasing settlement and suburban development.

Teasing apart these variables, such as the role of the natural setting, is clearly a priority for further work on urban–rural gradients. Bell (1986), for example, has suggested that urbanization in a tropical rain forest may have different effects on local species richness than urbanization in other natural settings, because rain forest birds have exceptional difficulty adapting to human settlements.

Local extinctions during housing development.

Areas of active development tend to have low biodiversity because of the devastating impact on native species of most residential and commercial development methods. Before construction of most residential and commercial buildings, it is common for developers to remove most vegetation and even topsoil (Sharpe et al. 1986). This reduces construction costs by allowing equipment ready access to the construction site.

A study of the fate of natural vegetation during urban development in Wisconsin found that only about one-third of the original vegetation was not destroyed (Sharpe et al. 1986). The loss of native vegetation (and total vegetated area) has a negative impact on native animal diversity. Bird species richness declined dramatically in the early stages of housing construction (compared to preconstruction diversity) in California (Vale and Vale 1976) and Poland (Luniak 1994).

Once construction is finished, some of the area is paved, which removes it as habitat for nearly all species. In Palo Alto, California, for example, 25% of the area of residential communities is covered by pavement (Blair and Launer 1997); another 20% of the area is covered with housing. Of the remaining nonpaved portions, much is replanted with (usually nonnative) grasses, shrubs, and trees (Wasowski and Wasowski 2000).

Conservation strategies. Habitat conservation can utilize preservation and restoration (figure 2). The most effective (and cheapest in the long term) strategy is to preserve as much remnant natural habitat as possible. Many studies describe how native species richness in a remnant habitat increases with the area of that habitat. This is true for many taxa,

including birds (Tilghman 1987), mammals (Dickman 1987), and plants (Dawe 1995).

One way to preserve remnants in housing developments is to retain predevelopment vegetation. A number of recent books, such as *The Landscaping Revolution* (Wasowski and Wasowski 2000), have pointed out the benefits of retaining pre-existing vegetation when building new homes. Unfortunately for conservation goals, this type of construction is rarely undertaken by most residential real estate developers. Although ostensibly related to cheaper costs of mass construction, retaining more predevelopment vegetation is less expensive in the long term (Dorney et al. 1986) and is preferred by many homeowners (Wasowski and Wasowski 2000).

A major influence on natural remnants is the matrix, or the type of habitat, that surrounds them. Remnants are often embedded in a highly disturbed matrix that also serves as a continuous source of nonnative species. A major challenge is that remnant habitats are open to colonization by nonnative species of invasive plants (Luken 1997) and predatory animals such as housecats and dogs (Marzluff 2001). These nonnative invaders and predators can greatly reduce the ability of the remnant habitat to support native species, especially birds. In the language of population biology, these remnants become population “sinks” that are unable to support self-sustaining populations of the native species.

Restoration strategies: Succession and cultivation.

Conservation strategy can also focus on restoring native species in managed and ruderal habitats. In natural ecosystems, biotic succession increases the number of plant and animal species after a disturbance (Gibson et al. 2000). This is also true of ruderal and managed habitats that remain undisturbed long enough for succession to occur. Various studies have documented how succession increases species diversity in ruderal and managed communities, for example, increased plant diversity in urban lots (Crowe 1979), increased arthropod diversity in restored communities (Majer 1997), and increased bird species richness in residential communities (Vale and Vale 1976, Munyenembe et al. 1989, Luniak 1994). As a consequence, older residential areas (usually nearer the urban core) tend to have higher species richness than younger ones (e.g., Munyenembe et al. 1989).

The studies cited above show that the accumulation rate of new species during succession is initially very rapid and is substantially slower after the first few years and especially after the first decades. Aside from increasing total diversity, ecological succession also often reduces the diversity of nonnative species in an area (Gibson et al. 2000), many of which rely on disturbance to sustain their populations (Luken 1997).

Another restoration strategy to increase native biodiversity in managed habitats is to cultivate a variety of plant species. Cultivation with native plant species may benefit not only native plant populations but also native animal populations. For example, native bird species richness in Australia (Munyenembe et al. 1989) and North America (Sears and Anderson 1991) tends to positively correlate with the volume and species

diversity of native vegetation. Similarly, the percentage of native insect species in a fauna has been found to correlate with the percentage of native plant species (Crisp et al. 1998). Landscaping golf courses with native plants can benefit many local native bird species (Terman 1997).

Compositional changes along the urban–rural gradient

Species vary in their ability to adapt to the often drastic physical changes along the urban–rural gradient (Gilbert 1989, Adams 1994). Although there are probably many ways to categorize these changes in species composition, many bird (e.g., Goldstein et al. 1986, Maeda and Maruyama 1991, Blair 2001) and mammal (e.g., Nilon and VanDruff 1987) studies have concluded that species along the gradient can be classified, for convenience, into three distinct categories reflecting their reaction to human activities. Using Blair's (2001) terms, these categories are "urban avoiders," "urban adapters," and "urban exploiters" (figure 2). While birds are the best-studied taxa for work on urban–rural gradients, these three categories have also been used for work on butterflies (Blair and Launer 1997) and lizards (Germaine and Wakeling 2000).

These categories show that, even in highly modified environments, species are nonrandomly assembled in ways that approximate community assembly processes in nature. Each of these assemblages has a distinctive set of ecological characteristics that reflect the impacts of urban sprawl on native species. One of the most important traits that separates the three categories is the extent to which species depend on human-subsidized resources to exist in an area (Johnston 2001). As subsidized resources increase toward the urban core, there is a concurrent increase in species that utilize them. Urban exploiters are generally commensals that are almost entirely dependent on human subsidies (i.e., obligate parasites). Urban adapters are able to utilize subsidies but are facultative in that they also widely use natural (wild-growing) resources. Urban avoiders tend to rely only on natural resources (Johnston 2001).

Characteristics of urban avoiders, adapters, and exploiters. Because birds, mammals, and, to a lesser extent, plants are the best-studied taxa along urban–rural gradients, they will be the major focus here. *Urban avoiders* are species that are very sensitive to human persecution and habitat disturbances. The first species to disappear in the proximity of humans are usually large mammals, especially predators, because they are actively persecuted, relatively rare, and have low reproductive rates. Thus, cougars, bison, and elk were among the first to disappear after European settlement began (Matthiae and Stearns 1981). Avian urban avoiders include species adapted to the interior of large, old forests, such as tree-foraging insectivores, neotropical migrants, and many ground-nesting birds that are very sensitive to the presence of humans and pets (Whitcomb et al. 1981, Beissinger and Osborne 1982, Sears and Anderson 1991, Adams 1994). Plant species that are very sensitive to human activities would include late-

successional (old-growth) and wetland plants (Stein et al. 2000), the loss of which is attributable to our tendency to clear forests and drain wetlands for agricultural and settlement goals.

Urban adapters are often found in the matrix of human land uses that occur in suburban landscapes. For plants, early successional species are common in managed suburban habitats, such as residential yards and commercial as well as unmanaged ruderal habitats (e.g., undeveloped lots). These early successional plants include both cultivated species favored by humans (e.g., turfgrass, fast-growing ornamental shrubs, and trees), as well as weedy species that are common in both managed and unmanaged suburban habitats. The most common weedy species are wind-dispersed lawn weeds (e.g., dandelions, crabgrass) and bird-dispersed invasive shrubs (e.g., privet, pokeweed) that commonly grow on cleared, untended landscapes (Crowe 1979). Botanically, suburban landscapes are often characterized as structurally approximating sparsely forested savanna or grassland communities (Dorney et al. 1984). This is apparently an aesthetically preferred landscape for most suburbanites (Henderson et al. 1998).

Among animals, urban adapters typically include many species often referred to as "edge species," which are adapted to forest edges and surrounding open areas (Whitcomb et al. 1981, Adams 1994). These animals exploit many foods, including human-subsidized foods, such as cultivated plants and garbage. The great abundance of such subsidized foods is one reason why these animal urban adapters often attain an abundance and biomass that is much greater than in natural areas (Adams 1994, Marzluff 2001). Another reason is that natural predators of these animals are usually eliminated by human activities (Gering and Blair 1999).

For birds, urban adapters include a high proportion of certain feeding guilds. These include omnivores and ground foragers, such as the American robin and many corvids (crows, jays); seedeaters such as finches; and aerial sweepers such as swifts (Whitcomb et al. 1981, Beissinger and Osborne 1982, Sears and Anderson 1991, Adams 1994, Johnston 2001). Each of these three guilds seems to be responding to different aspects of human impacts. The highly productive (i.e., fertilized) lawn and ornamental plant ecosystem provides a rich source of invertebrate and plant foods (Falk 1976) for ground gleaners, while seedeaters favor bird feeding stations and many ornamental plants that produce seeds (Adams 1994). Aerial sweepers take advantage of the many open areas, including pavement, over suburban habitats and the high abundance of many flying insects, especially those that are attracted to artificial lights. Tree, shrub, and cavity nesters are also common among urban adapters (Johnston 2001).

As most mammals lack the high mobility of flight possessed by birds, life in suburban environments poses different challenges. Nevertheless, mammalian urban adapters are able to find shelter from intensive human activity as well as exploit rich sources of food provided by humans (Matthiae and Stearns 1981, VanDruff and Rowse 1986, Nilon and VanDruff 1987). One group of mammalian adapters finds refuge

through their burrowing habits. Groundhogs, cottontail rabbits, moles, and skunks are examples of successful adaptation to human proximity in suburbia. Trophically, these animals derive much food from the rich subsidies of suburban lawns, including rapidly growing grasses, ornamental plants, and invertebrates (Falk 1976).

Another group of mammal adapters includes species that require adjacent forest fragments (e.g., in cemeteries and parks) for shelter (Dickman 1987). These species typically forage for human-subsidized food supplies in surrounding areas. Some are medium-sized omnivores (especially raccoons and opossums) that forage in garbage, vegetable gardens, and other resources provided by humans. Others are medium-sized carnivores, such as foxes and coyotes, that consume a wide variety of prey. As with birds, elimination of large predators (in addition to subsidized resources) leads to very high population densities of urban adapter mammal species (Crooks and Soulé 1999).

Urban exploiters, often called synanthropes (e.g., Sukopp and Werner 1982, Mackin-Rogalska et al. 1988, Johnston 2001), are very (often totally) dependent on human resources. The abundance of urban exploiters is usually not dependent upon the amount or types of vegetation (Lancaster and Rees 1979, Nilon and VanDruff 1987, Mackin-Rogalska et al. 1988, Johnston 2001). The combination of predator release (predator removal, such as the extermination of wolves and cougars) with abundant food subsidies allows them to attain enormous population densities (Lancaster and Rees 1979, Adams 1994).

Urban exploiters probably represent the most homogenized of the world's biotas (Blair 2001). Unlike urban adapters, which are largely composed of early successional species from nearby ecosystems, urban exploiters are composed of a very small subset of the world's species; these exploiters are well adapted to intensely modified urban environments wherever humans construct them across the planet (Adams 1994, Johnston 2001, Marzluff 2001).

Urban environments typically have more in common with other cities than with adjacent natural ecosystems (Sukopp and Werner 1982), so urban exploiters are often not native to a region (Adams 1994, Kowarik 1995, Blair 2001), but tend to leapfrog from city to city. Thus, rock doves, starlings, house sparrows, Norway rats, and the house mouse are found in all cities in Europe (Mackin-Rogalska et al. 1988) and North America (Adams 1994). This is also true for urban plants (Whitney 1985).

Among plants, urban exploiters tend to be ruderal species that can tolerate high levels of disturbance, especially grasses and annuals (see reviews in Sukopp and Werner 1982, Whitney 1985, Kowarik 1995). Examples include wind-dispersed weeds that colonize abandoned industrial and commercial properties and plants that can grow in and around pavement. Adaptive traits that are typical of urban-exploiting plants include tolerance to high levels of air pollution (especially smog and acidic fog); trampling; and alkaline, compacted, and nitrogenous soils.

Avian urban exploiters are often species evolutionarily adapted to cliff-like rocky areas and therefore are preadapted to the devegetated concrete edifices of very urbanized areas (Lancaster and Rees 1979, Adams 1994). Common examples include the rock dove and peregrine falcon. Another group of avian exploiters consists of cavity-nesting species that are able to inhabit human dwellings. Examples include the house sparrow, house finch, and European starling. Trophically, avian urban exploiters tend to be ground-foraging seedeaters or omnivores (Lancaster and Rees 1979, Adams 1994).

Mammalian urban exploiters find shelter in human dwellings and exploit the rich food sources in or near them. Trophically, they are usually omnivorous (Adams 1994) and include such familiar species as the house mouse, black or brown rat, and insects, including a variety of cockroach species.

Increasing nonnative species toward the city. Many studies have found that the number (and proportion) of nonnative species tends to increase along the urban–rural gradient, moving toward the urban center. In general, the proportion of species that is nonnative goes from less than a few percent in rural areas to over 50% at the urban core. These changing proportions apply to plants in the United States (Whitney 1985) and Europe (Kowarik 1995) and birds in the United States (Blair 2001). The population density of nonnative species—both mammals (Mackin-Rogalska et al. 1988) and birds (Marzluff 2001)—also tends to increase the nearer they are to the urban core.

The increase in nonnative species toward the urban core reflects a number of human causes. One is that higher human population densities nearer the urban core produce increasing importation (“propagule pressure”) of nonnative species, for example, the cultivation of nonnative plants (Mackin-Rogalska et al. 1988, Kowarik 1995). Another cause is the increasing amount of “disturbed” habitat toward the urban core, which provides opportunities for nonnative species of plants (Kowarik 1995, Luken 1997) and animals (Adams 1994, Marzluff 2001) that can utilize the new resources.

Conservation implications of compositional changes. In their book *Urban Nature Conservation*, Kendle and Forbes (1997) note that, as highly urbanized areas are generally occupied by species that thrive in the presence of humans, there will be relatively few rare native species of conservation concern in areas of high human population density. They review some examples, however, of rare species of insects and plants found in highly urbanized areas; habitat conservation and restoration could be planned for sites that harbor such species. Not surprisingly, most rare species in urbanized areas are found sites that have escaped high-intensity development (Godefroid 2001). Sites where rare species most commonly occur include city parks, cemeteries, railroad trackways, vegetated areas under transmission lines, and other public rights-of-way that are protected from development (Gilbert 1989, Kendle and Forbes 1997).

Aside from the conservation of rare native species, knowledge of the species composition of urban biodiversity can be very useful as an educational tool to better understand the natural world. An enhanced appreciation of nature by the 80% of the American public that lives in this environment could promote more effective political and economic action. Examples of such knowledge include better education of the public in the natural history of local species and problems with nonnative species (Kendle and Forbes 1997).

Conclusions

Urbanization is a rapidly growing cause of many environmental problems (Benfield et al. 1999). The impact of urbanization is documented in the growing literature on the urban–rural gradient. These studies show consistent changes in species richness and species composition along the gradient.

Species richness of many taxa often declines along the gradient, with the lowest richness to be found in the urban core. Urban planners should find ways to preserve biodiversity as cities expand outward and subsequently modify natural habitat. Such efforts would most likely focus on preserving as much remnant natural habitat as possible, as opposed to most current land development techniques, which remove most natural vegetation during construction.

Where intensive land development has already occurred, native animal biodiversity can be increased by revegetation with a diversity of native plant species. Protecting this revegetated habitat from disturbance to allow ecological succession will not only enhance plant and animal diversity but also tend to reduce the diversity of nonnative species. Unfortunately, most current landscaping tends to revegetate with nonnative plant species in unnatural spatial distributions (Henderson et al. 1998, Wasowski and Wasowski 2000) and arrests succession through the management of those ecosystems (at great financial cost; Kendle and Forbes 1997).

Species composition also shows pronounced changes along the urban–rural gradient. Most notable is that nonnative species become proportionately more common toward the urban core. Urban avoiders include native species such as large predators and forest-interior (especially insectivorous) birds that disappear quickly in the initial stages of suburban encroachment, unless special effort is made to retain large tracts of native habitat and reduce human persecution of species.

Urban adapters, mammals and birds that are mainly adapted to forest edges and open areas, flourish in suburban habitats, especially older subdivisions where ecological succession has advanced and produced extensive revegetation. Urban adapters are very important for biodiversity education, because half of the American public lives in a suburban environment (USCB 2001). Public biodiversity education would be most effective if we draw on these familiar suburban community assemblages and species to promote an understanding of concepts such as ecological succession and the role of native plants in promoting native animal diversity. Because of its enormous size, wealth, and political influence, a more

ecologically informed suburban population could greatly improve the social support for conservation of native species in all ecosystems.

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