Conserving Biodiversity in Urbanizing Areas: Nontraditional Views from a Bird's Perspective

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Abstract

We review common population and community-level responses of wildlife to urbanization, and discuss how: (1) the amount and configuration of land cover and land use, and (2) the alteration of resources (e.g., type of vegetation, presence of food and water) and processes (e.g., natural disturbance regimes, species interactions, intensity of human recreation) within built environments influence animals, with special emphasis on birds. Although each landscape presents unique opportunities and constraints, we suggest that all urban areas have the potential to contribute to the conservation of biodiversity. The ecological value of urban areas may be promoted if planners, managers, and homeowners consider ways to (1) encourage retention and protection of natural habitats within urbanizing landscapes, (2) plan explicitly for open spaces and natural habitats within new subdivisions, (3) use a variety of arrangements of built and open space within developments, (4) enhance and restore habitat within open spaces, (5) improve quality of developed lands (i.e., the urban matrix) rather than directing management efforts only towards parks, reserves, and open areas, and (6) celebrate urban biological diversity to foster connections between people and their natural heritage.

Keywords

Biodiversity; birds; breeding; species richness; urbanization; urban planning.

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INTRODUCTION

Traditionally the conservation of biodiversity was widely viewed as an effort that should be focused most heavily, if not exclusively, on wildlands, parks, and other natural areas. However, this traditional perspective has grown problematic for an urbanizing world. Within a 50-year period (1950-2000), for example, the conterminous United States saw a doubling of land settled at urban densities (>1 housing unit/acre) and a five-fold increase in land settled at exurban densities (1 unit/1-40acres) (Brown et al. 2005). Thus, successful conservation of the world's biodiversity must include urban and urbanizing landscapes in addition to natural areas. Scientists, managers, and environmentalists now recognize the need to work closely with planners, policy-makers, homeowners and developers to identify ways that urban development can better incorporate the maintenance of ecological value.

Maintaining ecological function in urban developments can be addressed in part by designing and managing landscapes in an ecologically sensitive fashion. Various aspects of this approach, dubbed ecological landscaping, are considered elsewhere in this issue. We review the integration of conservation science with urban planning, relying heavily on our own experiences in Ohio and Washington State to illustrate how ecological landscaping can be used to maintain biological diversity in urban developments.

Conservation science is beginning to inform urban planning. Early suggestions by Leedy and Adams (1984), Adams and Dove (1989), Soulé (1991), Shafer (1997), and Donnelly and Marzluff (2004) focused mainly on the size, configuration, connectivity, and quality (e.g., type of vegetation and presence of predators) of reserves for sensitive species living in human-dominated settings. These authors suggested that urban reserves should be large with reduced edge-to-area ratio, situated in biodiverse "hotspots", comprised of structurally diverse native vegetation with intact native predator communities, and incorporate, rather than exclude, human community needs. Adams (1994), Marzluff and Ewing (2001), Marzluff and Bradley (2003) and Blewett and Marzluff (2005) went beyond reserves to consider planning, restoration, and education strategies in developments. These authors offered general recommendations, such as discouraging lawns while restoring shrub layers under urban forests, maintaining snags for cavity-nesting birds, preserving small wetland complexes, and involving residents in restoration projects. Moreover, the authors provided a number of specific recommendations intended for regional implementation (e.g., maintain large alders in northwestern US forests and oaks in southwestern US forests).

In this paper, we build upon these previous works by considering a variety of decisions routinely made by planners that have the potential to dramatically affect the conservation consequences of development. We first review the common population and community-level responses of wildlife to urbanization. Second, we discuss how the following two key development attributes influence animal communities: (1) the amount and configuration of land cover and land use, and (2) the alteration of resources (e.g., type of vegetation, presence of food and water) and processes (e.g., natural disturbance regimes, species interactions, intensity of human recreation) within urbanizing environments. Finally, we use our insights from studying how birds respond to these key development attributes to suggest six recommendations that planners and landscape managers (and to a lesser extent homeowners) interested in conserving biodiversity in urban areas may want to consider.

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ANIMAL RESPONSES TO URBANIZATION

Not only does urban development have the potential to influence animal behavior (e.g., habituation to people, food preferences, singing behavior), but the direct and indirect effects of urbanization on wildlife also can increase or decrease the viability of animal populations by affecting reproduction, survival, immigration and emigration (Fig. 1). For example, climatic changes induced by urbanization at both local and global scales (Vitousek 1994; Dale 1997; Kuttler 2001) can affect species distributions if new climate conditions approach the physiological tolerance limits of some animals. Urban dwellers also directly affect wildlife by supplementing their basic needs, introducing exotic predators and competitors, persecuting wildlife "pests," and disturbing breeding, roosting, and foraging activities (Adams et al. 2005; Chace and Walsh 2006). In response, some species colonize cities or increase in density in urban landscapes (Parris and Hazell 2005), whereas others decline or go extinct (Donnely and Marzluff 2006). These dynamics are particularly well known for corvid birds (members of the Family Corvidae: jays, crows, ravens, magpies, and nutcrackers), which often colonize or increase in population density in urban areas because their survival, reproduction, or immigration increases in response to supplemental foods, ameliorated climates, reduced persecution, and altered predator communities (Jerzak et al. 2005; Marzluff and Angell 2005; Withey and Marzluff 2005).
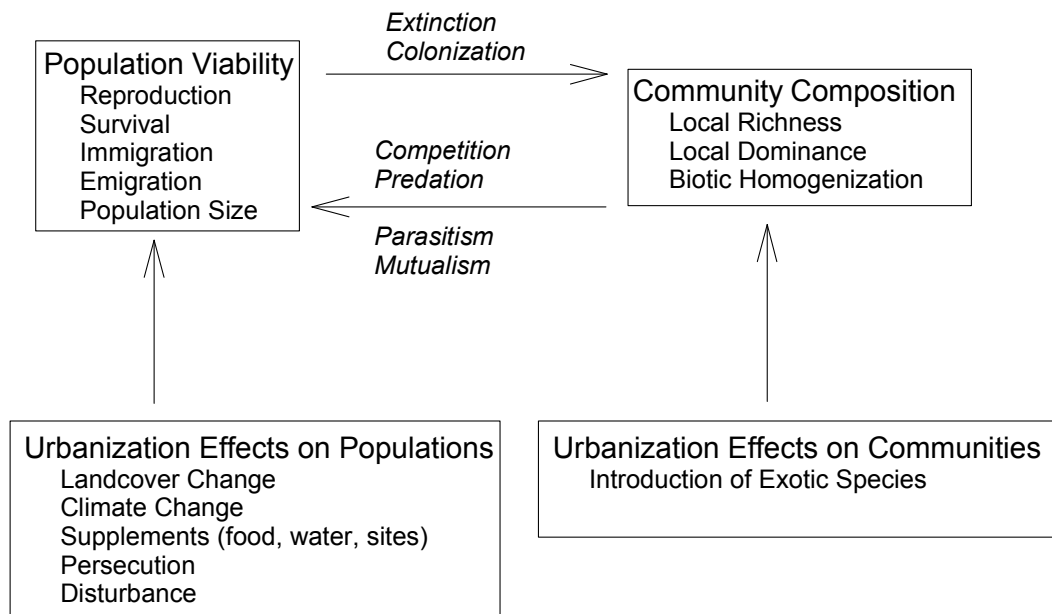

Figure 1. Conceptualization of how urbanization affects animal populations and communities. The extinction and colonization (or local extirpation and persistence) of species is a function of population size and they survival, reproduction, and movement of individuals in populations. Urbanization affects these aspects of a population and therefore influences community composition indirectly. Introduction of non-native species directly affects community composition. Community processes such as competition and mutualism also determine community composition by affecting population viability. The degree to which urban communities in a region or throughout the world come to resemble each other determines the degree to which biotic homogenization is increased by urbanization.

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Animals can be loosely categorized into three functional guilds based on their differing responses to urbanization—urban invaders, suburban adapters, and urban avoiders (Fig. 2; Blair 1996). Urban invaders (e.g., rock pigeon, Norway rat) are rare in natural areas and extremely abundant and fecund in urban areas (Fig. 2A). Suburban adapters (e.g., deer mouse *Peromyscus maniculatus*, coyote *Canis latrans*, black-headed grosbeak *Pheucticus melanocephalus*, American robin *Turdus migratorius*) are typically adapted to diverse, young, edge, and disturbed habitats. The close proximity of many vegetation types in moderately dense, suburban developments allows adapters to attain high density and probably high fitness in suburbs (Fig. 2B). Urban avoiders (e.g., Wilson's warbler *Wilsonia pusilla*, shrew-mole *Neurotrichus gibbsii*, many large carnivores) are sensitive to human activity and often specialize on interior habitats far from disturbance. They reach moderate density and attain high fitness in undisturbed, contiguous, native habitat (Fig. 2C). Although in some regions most Neotropical migratory birds fall into the urban avoider category and most resident birds are suburban adapters (Fig. 3, Rodewald and Bakermans 2006), bird responses to urbanization do not always parallel migratory guilds.
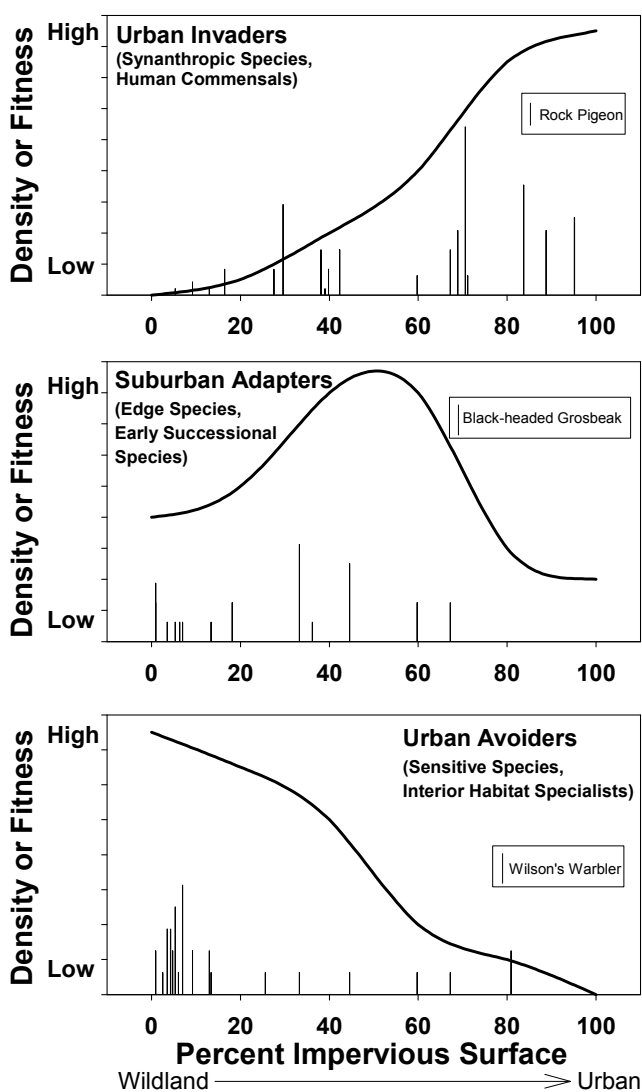
Figure 2. Generalized responses of populations or individuals to urbanization. The density of populations or fitness of individuals that invade (A), adapt to (B), or avoid (C) urban areas is shown as a function of the amount of impervious (sealed) surface in the landscape. Actual abundance data for birds in Seattle, Washington, USA that follow each pattern are plotted in histogram format with each curve. Methods for collecting bird abundance are described in Donnelly and Marzluff (2004).

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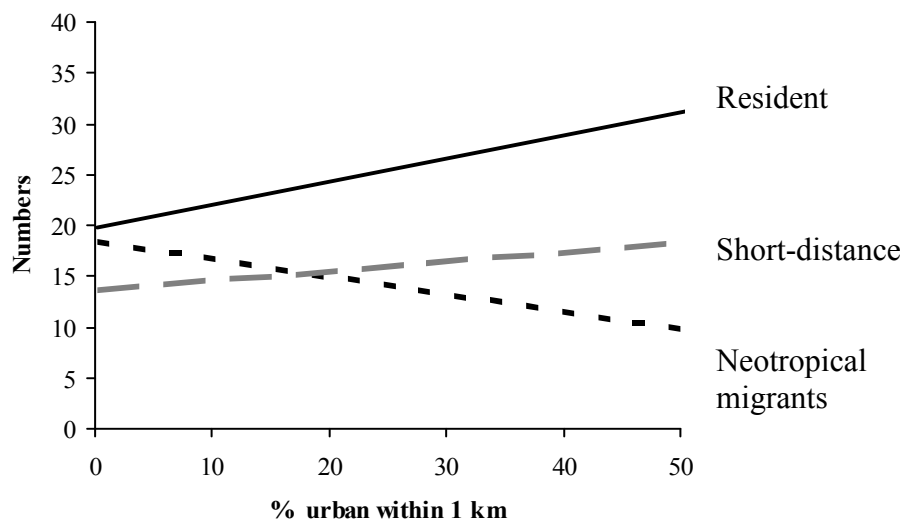
Figure 3. Response of avian migratory guilds to the percentage of urban development within 1 km of 33 riparian forest stands in central Ohio, 2001-2004. Methods described in Rodewald and Bakermans (2006).

As in any habitat, animal communities within urban areas are structured by the summed consequences of the ability of certain species to colonize the habitat as well as the likelihood that populations of various species will persist or go locally extinct. In this respect, urbanization affects animal communities in at least two integrated ways (Fig. 1). First, some populations persist in, or colonize, urban areas while others are extinguished. Second, humans augment the colonization of urban areas by purposefully or accidentally introducing species foreign to the locale. Together colonization, persistence, and extinction sum to determine how aspects of a community (its richness, balance, and uniqueness) vary along a gradient of urbanization (Marzluff 2005). For example, the number of species in a community (richness) is the dynamic balance among the invaders, adapters, and avoiders that occurs at any point along a wildland-to-urban gradient (Fig. 4).

The actual response of species richness to urbanization can take a variety of forms depending on the relative magnitude of extinction and colonization (Fig. 5). For example, as urbanization results in increasingly more impervious surface, the number of species may gradually decline if extinction rates are higher than colonization (Fig. 5A). Although this can occur if avoiders are the largest guild in a landscape because their abundance defines the majority of the community at each point along a wildland-to-urban gradient, it is relatively uncommon in nature. Rather, avoider species are oftentimes replaced by adapters and invaders such that the number of species remains similar across the gradient. Previous studies that documented a reduction in species richness with increasing urbanization may have failed to enumerate the full number of native and non-native species that colonize suburban and urban landscapes and, instead may have focused only on particular subsets, such as native species or forest interior species (Marzluff 2001).

A wide variety of recent studies on birds, mammals, fish, reptiles, and invertebrates have documented patterns of richness defined principally by high colonization rates of adapters (Fig. 5B; McKinney 2002; Sax and Gaines 2003; Blair 2004; Marzluff 2005). While many studies have documented peak richness in suburban landscapes, the magnitude and location of peak richness

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on a wildland-to-urban gradient may vary depending on the richness of the avoider guild, the similarity of suburban landscapes to wild landscapes, the diversity and magnitude of urban food and water subsidies, and the competitive and predatory effects of adapters and invaders (Marzluff 2005).
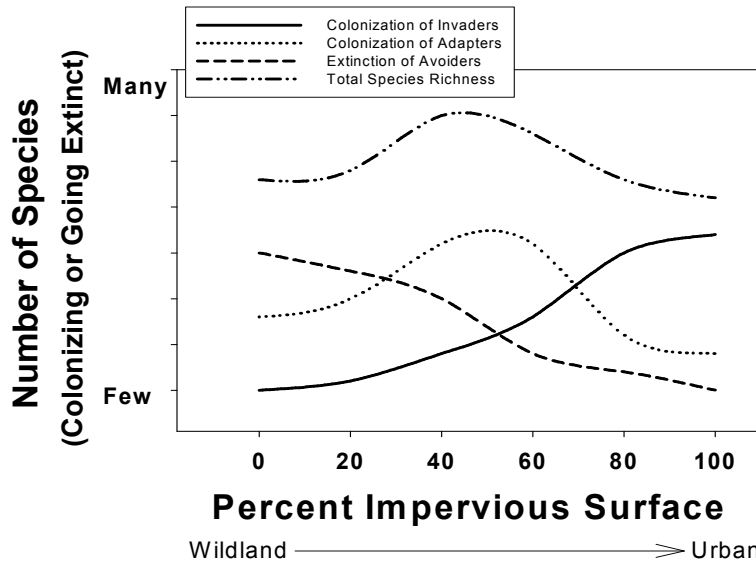
Figure 4. Hypothetical example of how colonization (or local persistence) of urban invaders and suburban adapters interacts with extinction (or local extirpation) of urban avoiders to determine changes in community diversity and composition along a gradient of urbanization. Community diversity increases where colonization of invaders and adapters outpaces extinction of avoiders (in suburban woods surrounded by about 40% impervious surface in the example). As diversity changes, the relative composition of the community also transitions from one comprised of mostly avoiders (0-20% impervious surface), through a balance of avoiders, adapters, and exploiters (30 – 60% impervious), to a community of mostly invaders (>70% impervious). Diversity in woods at any point on the gradient equals colonization – extinction as discussed for actual bird communities by Marzluff (2005).

Other fundamental patterns of animal communities are less well studied than richness (Marzluff 2001), but they often change in concert with it. Wildland communities, even if low in species richness, are not typically numerically dominated by one or a few very abundant species (an aspect of communities referred to as "evenness"). Urban communities, on the other hand, typically have less even distributions of animal abundance. Uneven urban communities are often dominated by a few species (e.g., rock pigeon, European starling, house mouse) that attain high density in response to abundant food, limited competition or predation, and ameliorated climate. Evenness is a relevant component of community diversity because, while uneven urban communities may have high richness, the preponderance of a few, very dense, species may make them less resilient to environmental change. Rare, but present, species may easily go extinct.

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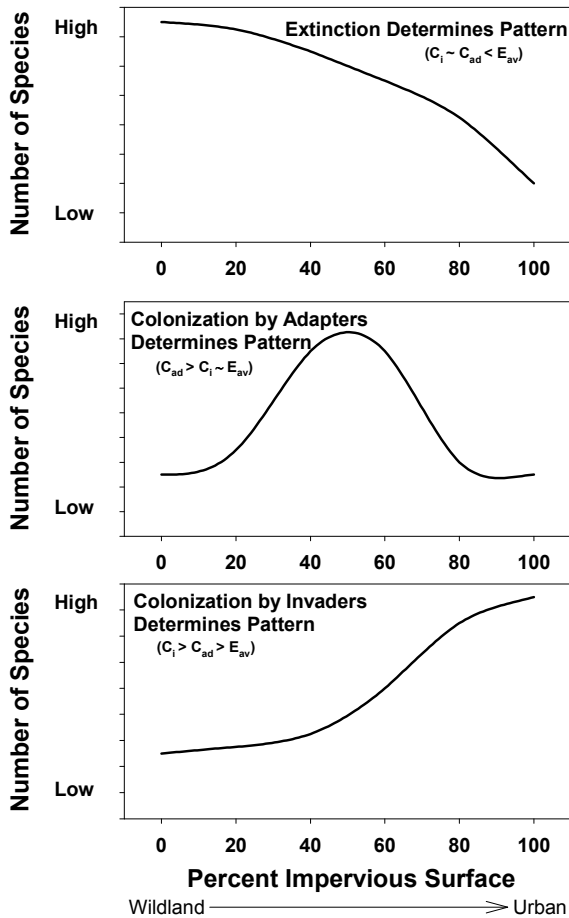
Figure 5. Changes in animal community diversity along gradients of urbanization. Diversity equals colonization – extinction as in Figure 4. The pattern of diversity along urban gradients depends on the relative importance of colonization and extinction. Where extinction dominates, diversity declines with urbanization (A). Where colonization by adapters dominates, diversity peaks in suburban landscapes rich in adapters (B). Where colonization by invaders dominates, diversity peaks in urban areas (C).

KEY URBAN DEVELOPMENT ATTRIBUTES THAT AFFECT BIOLOGICAL DIVERSITY

Change in amount and configuration of land cover types

As cities shrink or grow, the extent of various native and anthropogenic land covers ebb and flow. Commonly, native vegetation is lost, fragmented, simplified, and degraded as human settlement expands (Marzluff 2001). These changes in land cover, in turn, can alter geomorphology, disturbance regimes, hydrology, soil properties, and local climates of urban areas – all of which can influence local ecological communities (Marzluff et al. 2008). The extent to which conversion and rearrangement of land cover affects the dynamics of species' colonization and extinction determines the richness, evenness (or "relative dominance"), and composition of urban animal communities.

We suggest that the amount of particular land cover types primarily affects colonization by urban invaders and local extinction of urban avoiders. In both cases when the habitats upon which certain species depend (e.g., undisturbed native vegetation for the avoiders and anthropogenic settings for the invaders) are rare, extinction vortices (the consequences of rarity that reinforce each other as populations shrink, for example reduced reproduction leading to biased sex ratios which further reduce reproduction; Gilpen and Soulé 1986) may be common. Remnant urban avoider or small colonizing invader populations are especially vulnerable to

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extinction vortices when population sizes are small (Fernández-Juricic and Tellería 1999; Blewett and Marzluff 2005) or when predators or parasites reduce reproduction (Chace et al. 2003; Donnelly and Marzluff 2004; Sinclair et al. 2005) or survival (Breininger 1999), or humans disturb important life functions (Fernández-Juricic and Tellería 1999), provide inappropriate supplemental foods (Schoech and Bowman 2003), or construct barriers to emigration (Breininger 1999; St. Clair 2003). Population declines positively reinforce this suite of factors, resulting in accelerated decline of small populations to local extinction (Fernández-Juricic and Tellería 1999). Even where reproduction, survival, and dispersal appear unaltered by urbanization, extinction may occur in small populations (< a few hundred individuals) because of disrupted social behavior or environmental and demographic stochasticity (Lande 1993). Our studies with birds suggest that when less than one third of a landscape (within 1 km^2 in our studies) is urban or forest, then adapters (e.g., Fig. 2A) or avoiders (e.g., Fig. 2C), respectively, are often locally extinct (Blewett and Marzluff 2005; Donnelly and Marzluff 2006).

In contrast to local extinction rates, the pattern, especially the juxtaposition, of land covers is most likely to affect colonization by suburban adapters. These species typically use edges, aspects of multiple land covers, early successional lands, or frequently disturbed lands. As such, relative abundance and reproduction of many suburban adapters are positively related to juxtaposition of different vegetation types (Blewett and Marzluff 2005; Donnelly and Marzluff 2006; Hepinstall et al. in press). Colonization by suburban adapters is often high because urban landscapes include rich mixes of natural and artificial land covers resulting from the many actions of planners, landscape managers, and homeowners.

The combined influence of amount of each land cover type and their spatial patterns can determine the number and types of species that can be supported within a development. Species richness increases where colonization of invaders and adapters outpaces extinction of avoiders (up to about 40% impervious land cover on the example in Fig. 4), but it can quickly decline where extinction outpaces colonization. As diversity changes, the relative composition of the community also transitions from one comprised of mostly avoiders (0-20% impervious surface on Fig. 4), through a balance of avoiders, adapters, and exploiters (30 – 60% impervious, Fig. 4), to a community dominated by urban invaders (>70% impervious, Fig. 4). These changes in species composition can profoundly affect how species interact in ways that can affect the viability of populations, especially in cases where competition or predation pressures are intensified. This implies that in addition to land cover patterns, species interactions can affect the long-term persistence of species in urbanized landscapes.

The ability of suburban landscapes to provide a diversity of land covers, which vary in amount and pattern, likely explains why total biological richness often is highest in these settings. Because suburban landscapes have many juxtaposed land covers they can support substantial local populations of suburban adapters and may provide enough built areas to support viable populations of urban invaders. If substantial areas of unbuilt or open land are retained within or in close proximity to suburban developments, then some viable populations of tolerant urban avoiders may also persist.

Although patterns of animal diversity in urbanizing landscapes derive from intensive anthropogenic disturbance, community changes parallel responses of other ecological communities to disturbance regimes in more natural landscapes. In particular, the peak in animal richness in suburban landscapes is generally consistent with the intermediate disturbance hypothesis (Roxburgh et al. 2004), and is specifically consistent with the disturbance heterogeneity model (Porter et al. 2001). Intermediate disturbance, which is characteristic of suburban landscapes, produces a rich mix of natural and altered land covers and the resources

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contained therein. Each distinct land cover is inhabited by a unique set of animals. Such rich juxtaposition of diverse animal assemblages may be short-lived, if populations are dependent upon frequent colonization from increasingly distant lands, or they may persist indefinitely if sustained by locally high survival and reproduction. The heterogeneity in land cover produced and maintained by the disturbance of urbanization can lead to locally rich animal communities.

The patterns of community diversity discussed above are features of relatively local (city-sized) areas. Even if richness increases at moderate or extreme levels of land conversion (Fig. 5B, C), global or regional levels of diversity may decline. This reduction in global diversity at the hands of increased local diversity is a result of biotic homogenization, which occurs when once locally diverse areas across the world come to be composed of the same, tolerant, and competitive species (Lockwood et al. 2000; Lockwood and McKinney 2001; Olden and Poff 2003, 2004; Olden et al. 2004). Indeed, urban animal communities already share many species (Blair 2001; Clergeau et al. 2006; Devictor et al. 2006). But unless shared species exert strong effects on species unique to various landscapes (e.g., outcompeting or preying upon them), homogenization will remain incomplete (Marzluff 2005). This does not yet appear to be the case in most cities. Cities around the world often have a small subset of cosmopolitan species in common (e.g., house sparrows, European starlings, and rock pigeons), but contain many more unique species (Kelcey and Rheinwald 2005). Urban planners and landscape managers should strive to maintain the unique aspects of urban biotas.

**Alteration of resources and processes in urbanizing landscapes**

Urban development can mediate avian community structure by altering local resources, including habitat structure, microclimate, supplemental food, and abundances of predators and brood parasites (Marzluff et al. 2001, Faeth et al. 2005, Chace and Walsh 2006). While any of these individual factors has the potential to promote or discourage use of urban areas by particular species, multiple factors often act in concert. For example, the strong positive association observed between urbanization and numbers of an urban adapter, the northern cardinal (*Cardinalis cardinalis*), was likely a consequence of the fact that urban forests contained over twice as much fruit, birdfeeders, and preferred nesting substrate for cardinals than did rural forests (Leston and Rodewald 2006). Evidence of such resource-matching by urban adapters is further provided by Rodewald and Shustack (2008a), who showed that urban cardinals exhibited similar body condition and rates of survival and reproductive productivity to birds in more rural landscapes, despite maintaining up to four times higher population densities in urban than rural landscapes.

A number of urban-associated changes in the structure and floristic composition of vegetation can affect bird communities. Ecologists have long known that bird diversity is linked to plant communities (MacArthur and MacArthur 1961; James 1971; Roth 1976; James and Wamer 1982). Shifts in vegetation can be induced by hydrological changes associated with impervious surfaces which can increase erosion, destabilize streambanks, promote sedimentation, and even modify the water table (Pickett et al. 2001). Invasion of habitats by exotic plants seems to be an especially insidious problem in urban systems, as several studies suggest that the risk of invasion increases for forests near urban areas (Moran 1984; Nilsson et al. 1989; Hutchinson and Vankat 1997; Pysek et al. 2002, Borgmann and Rodewald 2005). Exotic plants are well known to disrupt ecosystem processes and shift floristic and faunal composition (Vitousek 1990; Wilcove et al. 1998; Ehrenfeld 2003). There also is evidence that exotic plants can alter species interactions at higher trophic levels, such as predator-prey relationships (Schmidt and Whelan 1999; Remes 2003; Borgmann and Rodewald 2004). In Ohio, for example, the exotic and invasive amur honeysuckle (*Lonicera maackii*) affected bird communities by providing the vast

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majority (>90%) of available fruits at sites during non-breeding seasons (Leston 2005), promoting a dense understory layer in riparian forests (Leston and Rodewald 2006), and inducing changes in nest placement (e.g., closer to the ground) in ways that increased the vulnerability of nests to predators (Schmidt and Whelan 1999; Borgmann and Rodewald 2004). Thus, maintaining a plant community comprised of native species may help to ameliorate some avian community responses to urbanization.

In addition to changes in local vegetation induced by urbanization, urban areas may provide new food sources or modify local climate in ways that influence birds. Supplemental food provided at feeding stations can affect distribution, abundance, habitat selection, annual survivorship, sociality, and foraging behavior of birds, especially during winter months (Brittingham and Temple 1988; Desrochers et al. 1988; Wilson 2001; Doherty and Grubb 2002; Atchison and Rodewald 2006). Effects of winter resources also can carryover to other seasons and influence the distribution of breeding birds, even though the resource may not be used at that time. For example, numbers of breeding American goldfinches (*Carduelis tristis)* and Carolina chickadees (*Poecile carolinensis)* in riparian forests of Ohio were best explained by numbers of nearby birdfeeders, a resource used almost exclusively in non-breeding seasons (Rodewald in press). Given the expected changes in food resources, it is not surprising then to see an increase in abundance of omnivorous species (i.e., species that consume both plant and animal matter), in contrast to the decrease in insectivorous species, as landscapes surrounding forests became more urbanized in Ohio (Rodewald in press, Fig. 6). Wintering birds in urban areas also are expected to benefit from elevated temperatures (i.e., the urban heat island effect) due to the combined effects of increased anthropogenic heating, decreased vegetated surfaces, and increased concrete and pavement (Botkin and Beveridge 1997). Warmer winter temperatures can improve the energetic environment for resident birds, especially for small-bodied species (Grubb 1975; Wachob 1996). Thus, the combination of supplemental food and altered microclimate may create habitats that are beneficial to urban birds in harsh winter climates.
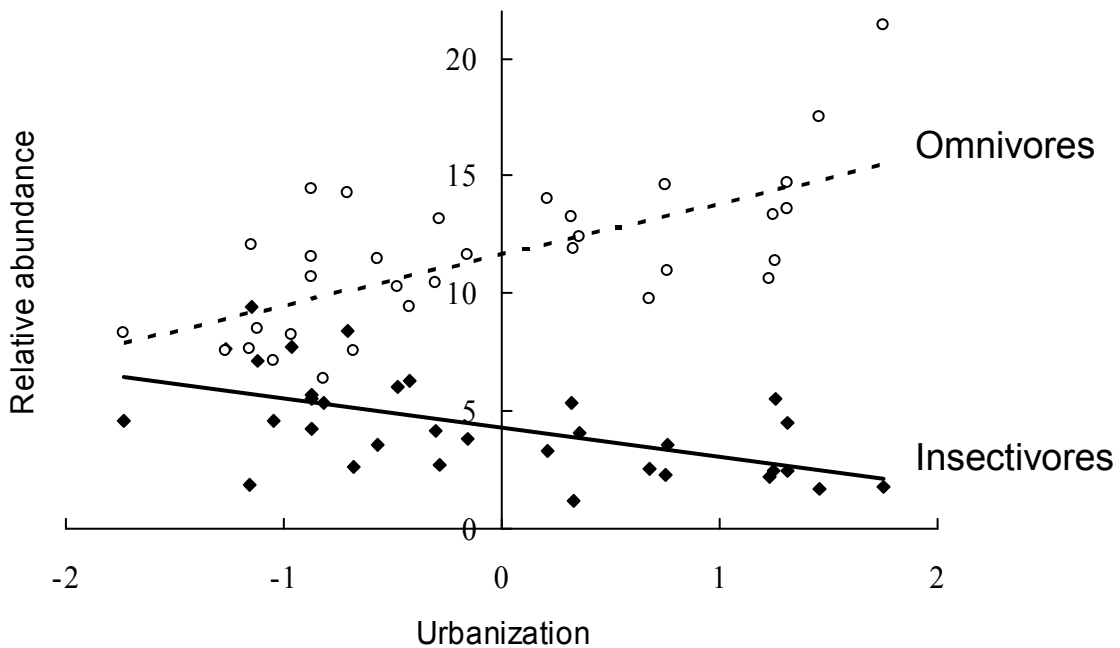
Figure 6. Changes in the abundance of birds with omnivorous or insectivorous diets in riparian forests located along a rural (negative numbers) to urban (positive numbers) landscapes in central Ohio, 2001-2004 (from Rodewald, in press).

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Whenever resources change, the nature of species interactions also has the potential to change. Although abundance of cowbirds and risk of parasitism are generally associated with agricultural landscapes (Robinson et al. 1995; Tewksbury et al. 1998; Smith and Wachob 2006), recent evidence suggests that residential and urban land uses also may increase the risk of brood parasitism (Tewksbury et al. 2006; Burhans and Thompson 2006; Marzluff et al. 2007; Rodewald and Shustack 2008b). Likewise, urbanization can strongly affect the composition and abundance of the predator community (e.g., Sorace 2002; Patten and Bolger 2003; Sinclair et al. 2005; Rodewald in press). As landscapes surrounding riparian forests in central Ohio became more urbanized, numbers of both avian and mammalian predators increased (Rodewald in press, Fig 7). Such changes in predator communities are frequently cited as causes of the commonly reported negative association between some sensitive Neotropical migratory species and urbanization, yet the link between urbanization and increased nest predation has surprisingly mixed empirical support from studies of natural nests (Phillips et al. 2005; Bakermans and Rodewald 2006; Burhans and Thompson 2006; Rodewald and Shustack 2008b). Most studies reporting higher rates of predation in urban environments have used artificial nests (Gering and Blair 1999; Jokimaki and Huhta 2000; Thorington and Bowman 2003; Jokimaki et al. 2005), which can result in biased estimates of nest predation due to species-specific responses of nest predators (Thompson and Burhans 2004). Our long-term studies of nest predation in central Ohio and western Washington suggest that nest predation in urbanizing landscapes show high temporal and spatial variability, and urbanization seems to be inconsistently related to daily mortality rates (Marzluff et al. 2007; A.D. Rodewald, unpublished data).
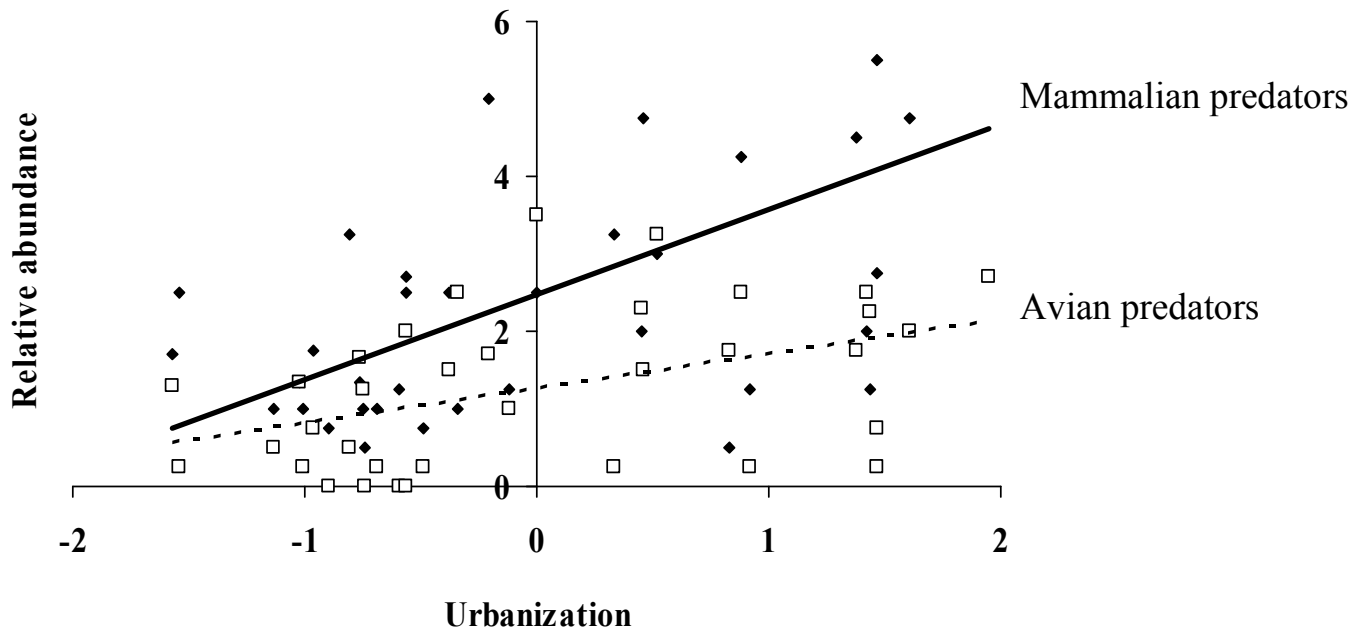
Figure 7. Numbers of mammalian and avian nest predators in riparian forests along a rural (negative numbers) to urban (positive numbers) landscapes in central Ohio, 2001-2004 (from Rodewald, in press).

Among the many local changes that accompany urbanization, recreational disturbance, especially through construction and use of trails, is one that is often overlooked. Although recreation-associated disturbance to animals is typically regarded as benign, recreational trails within parks may influence wildlife directly through disturbance by humans, pets, or predators (Gutzwiller et al. 2002; George and Crooks 2006; Marzluff and Neatherlin 2006) and indirectly

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through changes in the distribution of vegetation (Campbell and Gibson 2001; Thurston and Reader 2001; Dickens et al. 2005; Smith-Castro 2008). Even the location of dog-walking trails and leash-free zones may seriously affect bird use of parks, as dog-walking along woodland trails reduced the avian diversity by 35% and avian abundance by 41% (Banks and Bryant 2007). As a whole, there is limited and conflicting evidence showing higher rates of nest predation near trails. This inconsistency partly derives from the fact that trails may either promote or discourage predator activity depending on the species (Miller and Hobbs 2000; Sinclair et al. 2005), making it difficult to predict impacts to nesting birds. For example, Miller et al. (1998) documented greater nest predation in areas that contained recreational trails compared to those lacking trails, whereas Smith-Castro (2008) found evidence of a weak decline in nest predation near trails, likely stemming from higher nest height near trails. Interestingly, trails may affect nest-site selection, as nests near trails were surrounded by greater amounts of native vegetation and higher from the ground than expected compared to nests farther from trails (Smith-Castro 2008). In this way, recreational trails have the potential to indirectly influence reproductive behavior by altering nest site selection. Land managers and planners interested in bird conservation should consider potential impacts that may result from recreational activities and how alternative trail locations may affect wildlife.

WHAT CAN URBAN PLANNERS, DESIGNERS, AND POLICY MAKERS DO TO MAINTAIN BIOLOGICAL DIVERSITY IN URBANIZING LANDSCAPES?

Simply by virtue of the complex responses of animals to urbanization, we know that uniform strategies to protect the world's unique biological diversity in urbanized landscapes will be not be sufficient. Instead, a combination of reservation, restoration, and reconciliation (Rosenzweig 2003) strategies are needed to maintain diversity and nurture its connection to the people who must steward it. Biologists and land managers have suggested numerous recommendations intended to improve the ability of urban areas to contribute to biodiversity conservation at regional and local scales (e.g., Adams and Dove 1989; Soulé 1991; Shafer 1997; Marzluff and Ewing 2001; Adams et al. 2005). Collectively, these recommendations have emphasized either island biogeographic-based reserve design principles to increase effective area and reduce isolation (Soulé 1991, Shafer 1997) or local vegetation management to increase structural and floristic diversity of natural habitats (Leedy and Adams 1984; Blewett and Marzluff 2005). While these recommendations provide clear and useful direction to managers in a variety of contexts, we find that their broad application may not be sufficiently responsive to the complexity of the urban landscape matrix. Indeed, Pidgeon et al. (2007) recently showed that the complexity of urban landscape structure prevented the application of broad recommendations. Nevertheless, in the following section, we hope to build on previous recommendations by more explicitly recognizing the complexity of urban habitats and landscapes as we make suggestions to planners and policy makers.

Here we discuss strategies to conserve avian diversity that have become apparent in our research on North American birds in relatively recently urbanized forested and agricultural landscapes (Box 1). These six general principles offer guidance in reserving and restoring wildlife habitat in and around urbanized areas, and illustrate the importance of reconciling to conserve unique assemblages of plants and animals that often coexist in urban areas.

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1. Protect natural areas as parks or other open spaces within urbanizing landscapes in order to both (a) provide habitat to wildlife and (b) improve the quality of the landscape matrix.

Although some people may initially balk at the idea that urban parks and open spaces can support biodiversity, conserving biologically important areas within urbanizing regions can help to maintain populations of sensitive urban avoiders and may provide important colonization sources for surrounding neighborhoods. Although protecting the largest areas possible is ideal (Soulé 1991), even relatively small reserves can conserve many urban avoiders. For example, forest reserves of 42 ha in the urbanizing landscapes around Seattle contained reproducing populations of winter wrens, Pacific slope flycatchers, Wilson's warblers, black-throated gray warbers, and brown creepers (Donnelly and Marzluff 2004). Similarly, forested parks <10 ha in size in Columbus, Ohio can support sensitive species such as Acadian flycatcher, wood thrush, and yellow-throated warblers (Rodewald and Bakermans 2006).

Box 1. Recommendations to planners and policy-makers interested in promoting bird conservation in urbanizing landscapes.

1. **Protect natural areas as parks or other open spaces within urbanizing landscapes in order to both (a) provide habitat to wildlife and (b) improve the quality of the landscape matrix.** While preserving the largest contiguous areas of habitat possible is always advisable, simply increasing the amount of natural habitat within the landscape improves the ability of all habitat patches to support birds.

2. **Plan explicitly for open spaces and natural habitats within new subdivisions.** By carefully planning the amount and location of habitat within subdivisions, developments are more likely to capture inherently diverse areas and provide suitable habitat to birds.

3. **Within developments, use a variety of arrangements of built and open space.** Because species differ widely in their ecological requirements, no single habitat management approach will meet the needs of the regional suite of avian communities. Application of different management and design approaches ensures that a diversity of species will be supported.

4. **Enhance and restore habitat within existing open green spaces and natural areas.** Though birds generally respond positively to greater structural and floristic diversity of habitat, some species may require more deliberate management to provide their specific requirements (e.g., nest cavities).

5. **Improve habitat quality within the matrix of urban land uses rather than focusing only on management within parks, reserves, and open spaces.** Ultimately there will not be a sufficient number of reserves and parks to conserve biodiversity. Effective conservation requires that we think outside the park and explore creative ways to improve the habitat available to birds within the urban landscape itself.

6. **Celebrate urban biological diversity to foster connections between people and the natural heritage of their local ecosystems and regional biomes.** Not only does interaction with nature enrich our lives, but such interactions foster sensitivity to environmental issues – something needed as we face tremendous global change.

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Improving the quality of the landscape matrix is among the most important efforts that planners can undertake (Rodewald 2003). Landscape context can have a tremendous impact on bird conservation outcomes because the configuration and composition of the landscape can provide alternative habitat (Daily et al. 2001), can affect movements of individuals and dispersal through the landscape (Dunning et al. 1995; Gustafson and Gardner 1996; Belisle et al. 2001), can serve as a source of species and individuals invading habitat fragments, especially exotic species (Suarez et al. 1997; Pysek et al. 2002), and can even mediate edge, area, and isolation effects on bird (Donovan et al. 1997; Hartley and Hunter 1998). For example, in landscapes containing >30% remaining suitable habitat, the primary consequence of fragmentation is habitat loss, rather than area and isolation effects (Andrén 1994). As such, increasingly large patches are necessary to support area-sensitive birds in increasingly fragmented landscapes. An excellent example of this is Rosenberg et al. (1999), who found that area requirements of scarlet tanager (*Piranga olivacea)* varied by orders of magnitude depending on the amount of fragmentation in the landscape. In 2,500-acre landscapes with >70% forest only 66 acres were required for high suitability, whereas in landscapes with 40% forest 605 acres is needed (Rosenberg et al. 1999). Similarly, minimum area required for high habitat suitability for veery *(Catharus fuscescens)* ranged from 127 acres in forested landscapes (90%) to over 1004 acres in less forested landscapes (Rosenberg et al. 2003). Thus, the landscape context will likely constrain the ultimate effectiveness of any management activity regarding urban bird conservation.

2. Plan explicitly for open spaces and natural habitats within new subdivisions.

Retention of natural habitats generally improves the ability of urbanizing areas to contribute to biodiversity conservation, while at the same time providing an attractive option for homebuyers interested in supporting environmentally-sensitive developments and ensuring their access to open spaces and natural areas. Cluster development is one example of a design approach that can provide opportunity to maintain and plan for open space early in the process. Creative developers also have used natural habitats, such as wetlands and forests, to manage hydrology in subdivisions and reduce road construction needs. Policy-makers are advised to use caution that zoning restrictions regarding minimum lot size and housing density do not have unintentional consequences such as discouraging conservation-minded cluster developments. They also may consider incentives, such as fast-tracking permits, for developers who retain natural habitats within subdivisions. An important caveat is that application of cluster development designs alone does not necessarily ensure greater conservation value than traditional dispersed development (Lenth et al. 2006), as conservation value is determined by the types, amounts, and spatial configuration of habitat retained within developments. Moreover, no single design strategy can be universally applied, as the conservation value of any development depends on its ecological, social, and economic context. A coordinated, regional approach to cluster developments is the most successful strategy to promote the ecological value of natural areas within urban landscapes (Arendt 2003).

As part of the planning process within new developments, we suggest that planners consider open-space buffers around established and planned natural areas. The presence of residential and commercial development, even when localized, also can affect the ability of a manager to provide suitable habitat to some birds. Friesen et al. (1995) showed that adjacent land uses could be more important than patch sizes when they found that small woodlots lacking nearby houses had more diverse bird communities than large woodlots surrounded by houses in Ontario. Bird species richness, especially for Neotropical migratory species, decreased as urbanization increased in landscapes surrounding riparian forests (Rottenborn 1999; Hennings and Edge 2003; Miller et al. 2003, Rodewald and Bakermans 2006). Similarly, our ongoing research in urbanizing Midwestern landscapes demonstrates that the amount of urban

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development surrounding riparian forests is more closely associated with the bird community than the width (size) of the forest tract (Atchison and Rodewald, 2006; Rodewald and Bakermans, 2006). Species with other habitat affinities may show similar patterns. Haire et al. (2000) examined grassland open spaces of Boulder, Colorado, and found that the amount of urban development within a 96-acre landscape centered on the grassland was negatively related to abundance of several grassland-nesting birds. Accounting for potential impacts of urbanization on remnant habitats is especially important given the affinity of the public to live near forested areas (e.g., Kaplan and Austin 2004), which can result in comparably higher development rates near parks, state forests, and other natural areas.

3. Within developments, use a variety of arrangements of built and open space.

An overarching guide to maintaining biological diversity, especially in our urbanized landscapes, is to not do the same thing everywhere (Donnelly and Marzluff 2004 2006; Blewett and Marzluff 2005; Marzluff 2005). When each neighborhood has the same amount and configuration of built and open space, regional diversity may be reduced through the process of biotic homogenization. Thus, varying the density and configuration of housing between neighborhoods is an important step toward reducing homogenization. Densely built neighborhoods will support urban invaders. Low density neighborhoods may support urban avoiders, especially if the development that exists is spatially clumped together. Neighborhoods that purposefully intersperse built and open areas can support rich communities of native, suburban adapters. When neighborhoods of varying amount and configuration of development exist within a region, biodiversity will be maximized and residents will have a variety of opportunities to explore and engage a diverse nature around their homes. In Seattle, winter wrens and spotted towhees illustrate the potential tradeoffs among species that will be made if development is similar throughout a region. Reproductive success of wrens decreases in developments that replace forest cover with extensive lawns whereas that of towhees increases where forests are reduced (Fig. 8). Similarly, increasing numbers of buildings, roads, and lawn surrounding forested parks in Ohio was associated with declining reproductive productivity of Acadian flycatchers (Rodewald and Shustack 2008a) but no change in the productivity of the urban adapter, the Northern cardinal (Rodewald and Shustack 2008b). In some cases, though, we have discovered that fragmentation may actually increase the reproductive success of some native, shrub-nesting species (e.g., Swainson's thrush; Fig. 9). This counter-intuitive result makes sense in the urban forests of Seattle for Swainson's thrush because fragmentation can be associated with increased growth of salmonberry (*Rubus spectabilus*) hedges which are used for nesting and foraging by thrushes.

4. Enhance and restore habitat within existing open green spaces and natural areas.

Many simple habitat management strategies are useful within open spaces (Marzluff and Ewing 2001), including (1) increasing structural complexity with more cover and diversity of native understory plants (Donnelly and Marzluff 2006), (2) retaining and providing for the continued supply of snags (dead trees; Blewett and Marzluff 2005), (3) maintaining native predator communities (Soulé 1991), and (4) reducing barriers to movement. Decades of ecological literature demonstrate that the availability of nesting and feeding substrates contributes strongly to diversity and abundance of bird communities (MacArthur and MacArthur 1961; Roth 1976; James and Wamer 1982; Rotenberry 1985).

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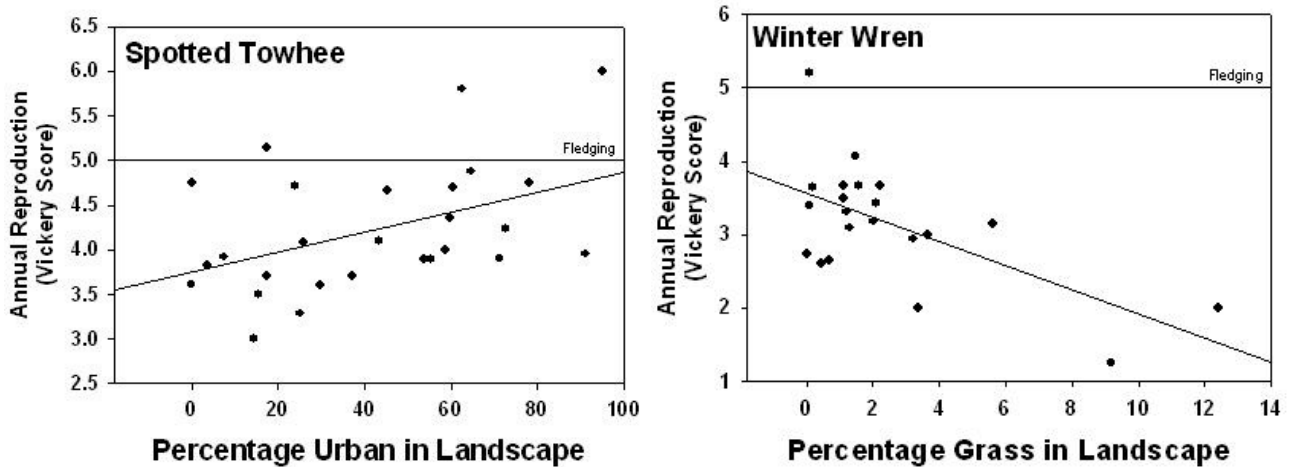
Figure 8. Opposing influences of development on reproductive success of two native songbirds in Seattle, WA. Each point is an independent study site comprised of a mixture of forest and residential development (described in Marzluff 2005). Reproductive success is measured as the average Vickery Index (Vickery et al. 1992) of pairs within study sites. We monitor pairs on territories throughout the breeding season and assign an annual Vickery Score to each territory as follows (1: only a singing male is observed; 2: a mated pair is observed; 3: evidence of nestbuilding or egglaying is observed; 4: evidence of nestlings is evident; 5: one brood of nestlings is successfully fledged; 6: a second nesting attempt is initiated after succeeding once; 7: successfully fledge two or more broods in a season).
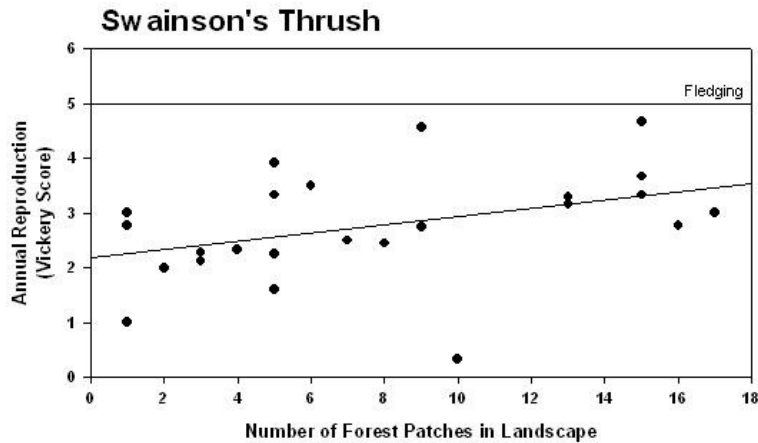
Figure 9. Increase in Swainson's thrush breeding success (measured using Vickery Index as in Fig. 8) with increased forest fragmentation due to urbanization in Seattle study areas.

5. Improve habitat quality within the matrix of urban land uses rather than focusing only on management within parks, reserves, and open spaces.

Suburban and urban lands can be restored to improve their capacity to maintain small populations of avoiders and viable populations of adapters. This will require the joint action of landscape mangers and homeowners. We have found that urban lands can be made more suitable for bird communities and other species by reducing both the amount of impervious surfaces (paved or built land) and replacing mowed lawn with more structurally complex landscaping elements (e.g., native shrubs, trees, and grasses). In cases where connectivity is thought to be

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important for population viability, improving the quality of the matrix has the additional benefit of facilitating movement of individuals among isolated remnant habitat patches. While we agree that in most cases increased connectivity among reserves and open areas is beneficial, this is not always the case in urban areas abutting wildlands. For example, cougars and black bears use such connections to invade suburban Seattle which often results in the death of the animal and negative public relations for wildlife in general.

6. Celebrate urban biological diversity to foster connections between people and the natural heritage of their local ecosystems and regional biomes.

Ultimately, conserving biological diversity in urban areas will require that we are open to novel solutions. Simply understanding that developed landscapes have conservation value is a leap for many natural resource managers and conservation biologists. But as our studies have shown, suburban landscapes often are extremely diverse and can be managed to facilitate survival of native species able to tolerate and adapt to human activity. Even urban landscapes can support a rich mix of native and non-native species. Species living in these extremely human-dominated landscapes should be celebrated (Rosenzweig 2003). Little management may be needed to maintain many of these unique, but hardy and common survivors. Rather than automatically focusing efforts on the removal of non-native urban species, and thereby reducing urban animal diversity, perhaps we should carefully consider the positive effects these animals have on people. The fact that most of the world's population resides in urban areas (Turner et al. 2004) means that we have opportunity and responsibility to facilitate positive interactions between humans and wildlife, particularly because these interactions may determine how humans value non-human life. Fostering the connection between people and the animals they live with may be important for human culture (Marzluff and Angell 2005), and the ability to conserve biological diversity beyond the city's influence. Strong citizen science programs will be needed to engage people with their local biological heritage. A full review of these is beyond our scope, but those interested can investigate successful (e.g., partnerships between the National Audubon Society and Cornell University, www.audubon.org/bird/citizen/) and proposed (e.g., a statewide program envisioned by the Washington Biodiversity Council; www.biodiversity.wa.gov) efforts.

CONCLUSION

Our review of wildlife responses to urbanization and development of six general guidelines to conserve biological diversity, with special focus on birds, in urbanizing areas combines three basic premises of conservation biology. The first two are traditional: reserve important habitats and restore those that have become degraded. While traditional cornerstones of conservation biology, our application of these strategies within urban landscapes is somewhat nontraditional. Although many conservation planners would bypass urban areas as targets worthy of conservation, we do not agree. Rather, we explicitly recognize that biological diversity is often locally high in and around urban areas, which is an important point to be made in our increasingly urban world. The third premise, reconciliation, is rather new (Rosenzweig 2003), but especially relevant in urban areas. Simply put, no amount of habitat protection or restoration will change the ecological reality of urban areas: cities are dominated by humans and, as such, include native and non-native species living in extremely modified environments. We suggest that conservation biologists, planners, and managers reconcile themselves to the fact that conserving biological diversity in urbanizing areas must include valuing novel associations of plants and animals. These novel associations have ecological and evolutionary significance (Marzluff in press), but most importantly enrich the lives of urban people and may kindle within them a value for biological diversity.

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ACKNOWLEDGEMENTS

LITERATURE CITED

Adams L.W. 1994. Urban Wildlife Habitats: A Landscape Perspective. University Minnesota Press, Minneapolis, MN. 208 pp.

Adams, L.H. and L.E. Dove. 1989. Wildlife reserves and corridors in the urban environment: a guide to ecological landscape planning and resource conservation. National Institute for Urban Wildlife, Columbia, Md. 91 pp.

Adams, L.K., L.W. VanDruff, and M. Luniak. 2005. Managing urban habitats and wildlife, pp. 714-730. In Braun, C. (Ed.). Techniques for Wildlife Investigation and Management. The Wildlife Society, Bethesda, Md.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Arendt, R.G. 2003. Linked landscapes: creating greenway corridors through conservation subdivision design strategies in the northeastern and central United States. Landscape and Urban Planning 68:241–269.

Atchison K.A. and A.D. Rodewald. 2006. The value of urban forests to wintering birds. Natural Areas Journal 26:280-288.

Bakermans M.H. and A.D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax virescens*) in central Ohio. Auk 123:368-382.

Banks P.B. and J.V. Bryant. 2007. Four-legged friend or foe? Dog walking displaces native birds from natural areas. Biology Letters 3:611-613.

Belisle, M., A. Desrochers, and M.J. Fortin. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82: 1893–1904.

18

Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506-519.

Blair, R.B. 2001. Creating a homogeneous avifauna, pp. 461-488. In Marzluff, J.M., R. Bowman, and R. Donnelly (Eds.). Avian conservation and ecology in an urbanizing world. Kluwer Academic Press. Norwell, MA.

Blair, R.B. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. Ecology and Society 9(5):2. http://www.ecologyandsociety.org/vol9/iss5/art2/ (accessed 06/12/2008)

Blewett, C.M. and J.M. Marzluff. 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. Condor 107:678-693.

Borgmann, K.L. and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: The role of exotic shrubs. Ecological Applications 14:1757-1765.

------. 2005. Forest restoration in urbanizing landscapes: Interactions between land uses and exotic shrubs. Restoration Ecology 13:334-340.

Botkin, D.B. and C.E. Beveridge. 1997. Cities as environments. Urban Ecosystems 1:3-19.

Breininger, D. R. 1999. Florida Scrub-jay demography and dispersal in a fragmented landscape. Auk 116:520-527.

Brittingham, M.C. and S.A. Temple. 1988. Impacts of Supplemental Feeding on Survival Rates of Black-Capped Chickadees. Ecology 69:581-589.

Brown, D.G., K.M. Johnson, T.R. Loveland, and D.M Theobald. 2005. Rural land-use trends in the conterminous United States, 1950-2000. Ecological Applications 15:1851-1863.

Burhans, D.E. and F.R. Thompson. 2006. Songbird abundance and parasitism differ between urban and rural shrublands. Ecological Applications 16:394-405.

Campbell, J.E. and D.J. Gibson. 2001. The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. Plant Ecology 157:23-35.

Chalfoun, A.D., F.R. Thompson, and M.J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306-318.

Chace, J.F., J.J. Walsh, A. Cruz, J.W. Prather, and H.M. Swanson. 2003. Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. Landscape and Urban Planning 64:179-190.

19

Marzluff and Rodewald: Conserving Biodiversity in Urbanizing Areas

Chace, J.F. and J.J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74: 46-69.

Clergeau, P., S. Croci, J. Jokimäki, M-L. Kaisanlahti-Jokimäki, and M. Dinetti. 2006. Avifauna homogenization by urbanization: analysis at different European latitudes. Biological Conservation 127:336-344.

Daily, G.C., P.R. Ehrlich, and G.A. Sanchez-Azofeifa. 2001. Countryside biogeography: utilization of human dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11: 1–13.

Dale, V.H. 1997. The relationship between land-use change and climate change. Ecological Applications 7:753-169.

Desrochers, A., S.J. Hannon, and K.E. Nordin. 1988. Winter Survival and Territory Acquisition in a Northern Population of Black-Capped Chickadees. Auk 105:727-736.

Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2006. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21:741-751.

Dickens, S.J.M., F. Gerhardt, and S.K. Collinge. 2005. Recreational portage trails as corridors facilitating non-native plant invasions of the Boundary Waters Canoe Area Wilderness (USA). Conservation Biology 19:1653-1657.

Doherty, P.F. and T.C. Grubb. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844-857.

Donnelly, R. and J.M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. Conservation Biology 18:733-745.

Donnelly, R. and J.M. Marzluff. 2006. Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. Urban Ecosystems 9:99-117.

Donovan, T.M., P.W. Jones, E. M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

Dunning, J.B., R. Borgella, K. Clements, and G.K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. Conservation Biology 9:542-550.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.

Faeth, S.H., P.S. Warren, E. Shochat, and W.A. Marussich. 2005. Trophic Dynamics in Urban Communities. Bioscience 55:399-407.

20

Fernández-Juricic, E. and J.L. Tellería. 1999. Recruitment patterns of blackbirds (Turdus merula in urban fragmented populations. Ardeola 46:61-70.

Friesen, L.E., P.F.J. Eagles, and R.J. Mackay. 1995. Effects of residential developments on forest-dwelling neotropical migrant songbirds. Conservation Biology 9:1408–1414.

George, S.L. and K.R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107-117.

Gering, J.C. and R.B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532-541.

Gilpin, M.E. and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction, pp. 19-34. In Soulé, M.E. (Ed.). Conservation Biology. Sinauer, Sunderland, MA.

Grubb T.C. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. Condor 77:175-182.

Gustafson, E.J., and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94–107.

Gutzwiller, K.J., S.K. Riffell, and S.H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. Journal of Wildlife Management 66:372-380.

Haire, S.L., C.E. Bock, B.S. Cade, and B.C. Bennett. 2000. The role of landscape and habitat characteristics in limiting abundance of grassland nesting songbirds in an urban open space. Landscape and Urban Planning 48: 65–82.

Hartley, M.J., and M.L. Hunter. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12:465–469.

Hennings, L.A. and W.D. Edge. 2003. Riparian bird community structure in Portland, Oregon: habitat, urbanization, and spatial scale patterns. Condor 105:288-302.

Hepinstall, J.A., J.M. Marzluff, and M. Alberti. In Press. Predicting land cover change and avian community responses in rapidly urbanizing environments. Landscape Ecology.

Hutchinson, T.F. and J. L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conservation Biology 11:1117-1124.

James, F.C. 1971. Ordination of habitat relationships among breeding birds. Wilson Bulletin 83:215-236.

James, F. and N. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63:159-171.

21

Marzluff and Rodewald: Conserving Biodiversity in Urbanizing Areas

Jokimaki, J. and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838-847.

Jokimaki, J., M.L. Kaisanlahti-Jokimaki, A. Sorace, E. Fernandez-Juricic, I. Rodriguez-Prieto, and M.D. Jimenez. 2005. Evaluation of the "safe nesting zone" hypothesis across an urban gradient: a multi-scale study. Ecography 28:59-70.

Jerzak, L., B.P. Kavanagy, and T. Tryjanowski (Eds.). 2005. Ptake kurkowate Polski. Bogucki Wydawnictowo Naukowe, Poznán.

Kaplan, R. and M.E. Austin. 2004. Out in the country: sprawl and the quest for nature nearby. Landscape and Urban Planning 69:235-243.

Kelcey, J.G., and G. Rheinwald. (Eds.) 2005. Birds in European Cities. Ginster Verlag, St. Katharinen, Germany. 450 pp.

Kuttler, W. 2001. Urban climate and global climate change, pp 344-350. In Lozan, J., H. Grassl, and P. Hupfer (Eds.). Climate of the 21st Century: Changes and Risks. Wissenschaftl. Auswertungen, Hamburg. 448 pp.

Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. American Naturalist 142:911-927.

Lande, R., S. Engen, and B-E Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford. 224 pp.

Leedy, D. L. and L. W. Adams. 1984. A Guide to Urban Wildlife Management. National Institute for Urban Wildlife. Columbia, Md. 42 pp.

Lenth, B.A., R.L. Knight, R.L., and W.C. Gilgert. 2006. Conservation value of clustered housing developments. Conservation Biology 20: 1445-1446.

Leston, L.F.V. 2005. Are Urban Riparian Forests Ecological Traps for Understory Birds? Habitat Selection by Northern Cardinals (*Cardinalis cardinalis*) in Urbanizing Landscapes., M.Sc. ed. The Ohio State University, Columbus, OH.

Leston L.F.V. and A.D. Rodewald. 2006. Are urban forests ecological traps for understory birds? An examination using Northern cardinals. Biological Conservation 131:566-574.

Lockwood, J.L, Brooks, T.M., and M.L. McKinney. 2000. Taxonomic homogenization of the global avifauna. Animal Conservation 3:27-35.

Lockwood, J.L., and M.L. McKinney (Eds.). 2001. Biotic Homogenization. Kluwer Academic / Plenum Publishers, New York, NY. 292 pp.

22

MacArthur R. and J. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Marzluff, J.M. 2001. Worldwide urbanization and its affects on birds, pp/ 19-47. In Marzluff, J. M., R. Bowman, and R. Donnelly (eds.). Avian Conservation and Ecology in and Urbanizing World. Kluwer Academic Publishers, Norwell, MA. 585 pp.

Marzluff, J.M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8:155-175.

Marzluff, J.M. In press. Urban evolutionary ecology. Studies in Avian Biology.

Marzluff, J.M. and T. Angell. 2005. In the Company of Crows and Ravens. Yale University Press, New Haven, CT. 412 pp.

Marzluff, J.M. and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. Restoration Ecology 9:280-292.

Marzluff, J.M. and G.A. Bradley. 2003. Ecological restoration in the settled-wildland interface. Pages 353-370. In Friederici, P. (Ed.). Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press. 582 pp.

Marzluff J.M. and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. Biological Conservation 130:301-314.

Marzluff, J.M., J.C. Withey, K.A. Whittaker, M.D. Oleyar, T.M. Unfried, S. Rullman, S., and J. DeLap. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. Condor 109:516-534.

Marzluff, J.M., E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, U. Simon, and C. ZumBrunnen. (Eds.). 2008. Urban Ecology: an international perspective on the interaction between humans and nature. Springer, New York. 807 pp.

McKinney, M.L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883-890.

Miller, J.R. and N.T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning 50:227-236.

Miller, S.G., R.L. Knight, and C.K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8:162-169.

23

Marzluff and Rodewald: Conserving Biodiversity in Urbanizing Areas

Miller, J.R., J.A. Wiens, N.T. Hobbs, and D.M. Theobold. 2003. Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecological Applications 13:1041-1059.

Moran, M.A. 1984. Influence of Adjacent Land-use on Understory Vegetation of New-York Forests. Urban Ecology 8:329-340.

Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant-species richness along riverbanks. Ecology 70:77-84.

Olden, J.D. and N.L. Poff. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. The American Naturalist 162:442-460.

Olden, J.D. and N.L. Poff. 2004. Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. Ecology 85:1867-1875.

Olden, J.D., N.L. Poff, M.R. Douglas, M.E. Douglas, and K.D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18-24.

Parris, K.M. and D.L. Hazell. 2005. Biotic effects of climate change in urban environments: The case of the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne, Australia. Biological Conservation 124:267-276.

Patten, M.A. and D.T. Bolger. 2003. Variation in top-down control of avian reproductive success across a fragmentation gradient. Oikos 101:479-488.

Phillips J., E. Nol, D. Burke, and W. Dunford. 2005. Impacts of housing developments on wood thrush nesting success in hardwood forest fragments. Condor 107:97-106.

Pickett S.T.A., M.L. Cadenasso, J.M. Grove, C.H. Nilon, R.V. Pouyat, W.C. Zipperer, and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.

Pidgeon, A.M., V.C. Radeloff, C.H. Flather, C.A. Lepczyk, M.K. Clayton, T.J. Hawbaker, and R.B. Hammer. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications 17: 1989-2010.

Porter, E.E., B.R. Forschner, and R.B. Blair. 2001. Woody fragmentation and canopy fragmentation along a forest-to-urban gradient. Urban Ecosystems 5:131-151.

Pysek P., V. Jarosik, and T. Kucera. 2002. Patterns of invasion in temperate nature reserves. Biological Conservation 104:13-24.

24

Remes V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conservation Biology 17:1127-1133.

Robinson S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional Forest Fragmentation and the Nesting Success of Migratory Birds. Science 267:1987-1990.

Rodewald, A.D. In press. Evaluating potential mechanisms that guide avian community response to urbanization. Studies in Avian Biology.

------ 2003. The importance of land uses within the landscape matrix. Wildlife Society Bulletin 31:586-592.

Rodewald A. and D. Shustack. 2008a. Consumer resource matching in urbanizing landscapes: are synanthropic species over-matching? Ecology 89:515-521.

------. 2008b. Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77:83-91.

Rodewald A.D. and M.H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? Biological Conservation 128:193-200.

Rosenberg, K.V., R.S. Hames, R.W. Rohrbaugh, Jr., S. Barker Swarthout, J.D. Lowe, and A.A. Dhondt. 2003. A land manager's guide to improving habitat for forest thrushes. The Cornell Lab of Ornithology. 32 pp.

Rosenberg, K.V., R.W. Rohrbaugh, Jr., S.E. Barker, J.D. Lowe, R.S. Hames, and A.A. Dhondt. 1999. A land manager's guide to improving habitat for scarlet tanagers and other forest-interior birds. Cornell Lab of Ornithology, Ithaca, New York, USA. 24 pp.

Rosenzweig, M.L. 2003. Win-win Ecology. Oxford University Press, Oxford. 236 pp.

Rotenberry, J.T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213-217.

Rottenborn, S.C. 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation 88:289-299.

Roth R.R. 1976. Spatial Heterogeneity and Bird Species-Diversity. Ecology 57:773-782.

Roxburgh, S.H., Shea, K., and J.B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359-371.

Sax, D.F. and S.D. Gaines. 2003. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18:561-566.

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Schmidt K.A. and C.J. Whelan. 1999. Effects of exotic Lonicera and Rhamnus on songbird nest predation. Conservation Biology 13:1502-1506.

Schoech, S. and R. Bowman. 2003. Does differential access to protein influence differences in timing of breeding of Florida Scrub-jays in suburban and wildland habitats? Auk 120:1114-1127.

Shafer, C.L. 1997. Terrestrial nature reserve design at the urban/rural interface. Pp 345-378. In. Conservation in highly fragmented landscapes. M. W. Schwartz (ed.). Chapman and Hall, New York.

Sinclair K.E., G.R. Hess, C.E. Moorman, and J.H. Mason. 2005. Mammalian nest predators respond to greenway width, landscape context and habitat structure. Landscape and Urban Planning 71:277-293.

Smith, C.M. and D.G. Wachob. 2006. Trends associated with residential development in riparian breeding bird habitat along the Snake River in Jackson Hole, WY, USA: Implications for conservation planning. Biological Conservation 128:431-446.

Smith-Castro, J. 2008. Impacts of recreational trails on breeding birds in forested urban parks. Columbus, OH: The Ohio State University.

Sorace, A. 2002. High density of bird and pest species in urban habitats and the role of predator abundance. Ornis Fennica 79:60-71.

Soulé, M.E. 1991. Land use planning and wildlife maintenance: guidelines for conserving wildlife in an urban landscape. APA Journal Summer:313-323.

St. Clair, C.C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. Conservation Biology 17:1151-1160.

Suarez, A.V., K.S. Pfenning, and S.K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology 11:928–935.

Tewksbury, J.J., S.J. Hejl, and T.E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.

Tewksbury, J.J., L. Garner, S. Garner, J.D. Lloyd, V. Saab, and T.E. Martin. 2006. Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759-768.

Thompson, F R. and D.E. Burhans. 2004. Differences in predators of artificial and real songbird nests: Evidence of bias in artificial nest studies. Conservation Biology 18:373-380.

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Thorington, K.K. and R. Bowman. 2003. Predation rate on artificial nests increases with human housing density in suburban habitats. Ecography 26:188-196.

Thurston, E. and R.J. Reader. 2001. Impacts of experimentally applied mountain biking and hiking on vegetation and soil of a deciduous forest. Environmental management 27:397-409.

Turner, W. R., Nakamura, T., and M. Dinetti. 2004. Global urbanization and the separation of humans from nature. BioScience 54:585-590.

Vickery, P.D., M.L. Hunter, and J.V. Wells. 1992. Use of a new reproductive index to evaluate relationships between habitat quality and breeding success. Auk 109:697–705

Vitousek, P.M. 1990. Biological invasions and ecosystem processes - towards an integration of population biology and ecosystem studies. Oikos 57:7-13.

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. Ecology 75:1861-1876.

Wachob, D.G. 1996. The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. Condor 98:114-122.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607-615.

Wilson, W.H. 2001. The effects of supplemental feeding on wintering Black-capped Chickadees (*Poecile atricapilla*) in central Maine: Population and individual responses. Wilson Bulletin 113:65-72.

Withey, J.C. and J.M. Marzluff. 2005. Dispersal by juvenile American Crows (*Corvus brachyrhynchos*) influences population dynamics across a gradient of urbanization. Auk 122:205-221.

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