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Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes

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Abstract. Urbanization is increasing worldwide with potentially important implications to biological diversity. I show that bird diversity is responsive to the reduction of forest cover associated with urbanization in the Seattle, WA, USA metropolitan area. Bird diversity peaks at intermediate levels of human settlement primarily because of the colonization of intermediately disturbed forests by early successional, native species. Extinction of native forest birds and colonization of settlements by synanthropic birds have lesser effects on the overall pattern of avian diversity with respect to the level of urbanization. However, extinction increases linearly with loss of forest and colonization by synanthropic species decreases curvilinearly with reduction of urbanization. These findings have biological, theoretical, and practical implications. Biologically, intermediate disturbance appears to drive diversity by increasing the heterogeneity of the local land cover. Theoretically, I present a graphical model and use it to derive testable hypotheses about how extinction and colonization are affected by urbanization to determine local diversity. Practically, maintaining high local diversity without reducing regional or global diversity will require planning so that the same landscapes are not promulgated everywhere. This will require cooperation among a diverse group of planners, ecologists, policy makers, home owners, educators, and activists.

Keywords: biological diversity, birds, colonization, disturbance, extinction, urban forests

Introduction

Increasing human population and associated industrialization has swelled our cities. In 1900 only 10% of humans lived in cities, but by 2000 nearly 50% did so, and 60% are expected to do so by 2030 (Sadik, 1999). Depending on economics, social preferences, and land use policies, the growth of urban populations causes cities, and even more profoundly their suburbs, to spread across large expanses of former agricultural and natural lands (Robinson *et al.*, 2005). The world-wide extent of sprawling settlement is obvious in nighttime images of Earth from space (Elvidge *et al.*, 1997). These images reveal that substantial portions of the north temperate zone are heavily settled, most ice-free coastlines are settled, our most fertile lands are quickly being developed, and overall about 3% of Earth's land area is urban (Lawrence *et al.*, 2002; Imhoff *et al.*, 2004). As human populations grow, the extent of urbanization will increase. But at what cost to biological diversity?

Human settlement has profound effects on the flora and fauna of a region. Settlements reduce native vegetation, sever connections among remaining native vegetation patches, and perforate large patches (Matlack, 1993; Robinson *et al.*, 2005; Hansen *et al.*, in press). Associated horticultural activities introduce exotics, degrade and simplify ground cover, and homogenize regional plant diversity (Reichard and White, 2001). Many animals, especially

those sensitive to predation, competition, and disturbance decline in response to these changes (Marzluff, 2001). The effects of urbanization are longer lasting and more extreme than those accompanying other anthropogenic land uses (Marzluff and Ewing, 2001), which may be why urbanization is a leading cause of species endangerment in the US (Czech and Krausman, 1997). However, for all its apparent evil, settlement benefits some wildlife by reducing predation, ameliorating climate, increasing available water, supplementing food resources, providing new nest sites, and increasing edge and vegetative diversity (Marzluff, 2001).

The varied influence of settlement on plant and animal populations affects emergent properties of communities, such as their biomass or diversity. Because some species that benefit from settlement often attain large population sizes, animal densities often increase with human settlement (DeGraaf and Wentworth, 1986; Blair, 1996; Sewell and Catterall, 1998; Donnelly and Marzluff, 2004a). Depending on the scale of inquiry, community diversity may increase, decrease, or remain unchanged in response to human activities such as urbanization (Olden and Poff, 2003; Olden *et al.*, 2004). Globally, diversity is decreasing across taxonomic groups (Pimm, 2001; Wilson, 2002; Sax and Gaines, 2003). Locally, however, diversity often increases as native species are joined by tolerant, cosmopolitan, and often exotic species (as summarized for fish, reptiles, mammals, and invertebrates by Sax and Gaines 2003). As native and exotic species interact through time, local diversity may decrease if exotic species drive native species to extinction (Scott and Helfman 2001). But if tolerant species simply replace sensitive ones, local diversity will remain unchanged for substantial lengths of time (Parody *et al.*, 2001). If land transformation increases habitat heterogeneity, and invading species do not dramatically consume or compete with native species, high local diversity may be maintained (Leopold, 1933; Blair, 1996, 2004; Porter *et al.*, 2001). This appears to be the case in Australian shrublands and Arizona grasslands, where bird communities were richest in suburban and exurban settlements, respectively (Sewell and Catterall, 1998; Zach Jones and Carl Bock, personal communication, 2004).

Understanding the processes controlling biological diversity in urbanizing landscapes may allow us to explain enigmatic results and anticipate the changes in diversity that accompany human settlement. MacArthur and Wilson (1963, 1967) identified the key processes governing biological diversity nearly four decades ago. In their models and empirical data, and in the rich literature that they spawned (notably Brown and Kodric-Brown, 1977; Lomolino 1999), diversity of an island or area was simply the balance between colonization and extinction. Colonization and extinction have historically responded to the demographic and life history characteristics of organisms, most notably their survival, reproduction, and dispersal (Marzluff and Dial, 1991; Marzluff *et al.*, 2000; Bolger, 2001). In today's human-dominated world, colonization and extinction are affected by direct and indirect human action. Extinction now occurs in response to land cover change or new selective forces applied by novel climatic regimes, predators, diseases, and competitors (Scott and Helfman, 2001; Sax and Gaines, 2003). Colonization is greatly accentuated as people remove barriers to dispersal, juxtapose a variety of land covers, and directly or indirectly introduce species outside of their native ranges (Kühn *et al.*, 2004). In a human-dominated world, diversity still emerges as the balance between extinction and colonization, but the amount, identity, and actions of invading species take on greater prominence (Olden and Poff, 2003, 2004).

In this paper I begin the process of understanding colonization and extinction in an urbanizing landscape. I extend the work of Donnelly and Blewett (Donnelly 2002; Donnelly and Marzluff, 2004a; Blewett and Marzluff, 2005) on bird communities in the Seattle, WA, USA metropolitan area. I determine the relative importance of colonization versus extinction to bird communities in Seattle and extend this observation to a general theory of avian diversity in urban habitat islands. By 'colonization,' I mean local additions to the avifauna by immigration and invasion of species not typical of local coniferous forests. By 'extinction,' I mean local extirpation (Olden and Poff, 2003; Sax and Gaines, 2003). I use my theory to suggest general planning and management considerations for those interested in maintaining biological diversity in urbanizing landscapes.

Methods

Study area

The Seattle metropolitan area (47°, 40' N; 122°, 20' W) is located within the Western Hemlock (*Tsuga heterophylla*) Zone of the Pacific Northwest (Franklin and Dyrness, 1988), where forest cover was dominant before European settlement (Booth, 1991). The metropolitan area inhabited by nearly 3 million people is composed of a large business district on the east side of the Puget Sound flanked by spawling residential developments and satellite business districts east into the Cascade Mountain foothills (figure 1).

Site selection

I selected 61 sites/landscapes representing the range and combination of habitat quantity (percent urban landcover) and habitat pattern (mean urban patch size, forest aggregation) by stratified random sampling. Details are in Donnelly (2002) and summarized here. I chose 1 km^2 as the standard landscape size because it was comparable to the size of typical residential developments and territories of common nest predators like the American crow (*Corvus brachyrhynchos*; Marzluff *et al.*, 2001a). I quantified habitat quantity and pattern from a classified 1998 LANDSAT satellite image (Botsford, 2000). Forest was ≥70% trees and <20% impervious surface (e.g., pavement). Urban forest was ≥25% trees and 20–60% impervious surface. Urban was ≥60% impervious surface. Other was ≥75% open water or bare soil. Throughout this paper when I refer to "forest" I am only referring to the "forest" category, not the "urban forest" category. Within each landscape, I estimated the representation of each landcover class and the size of urban patches (i.e., continuous urban areas) using the Geographic Resource Analysis Support System and the r.le add-on programs (Baker, 1997; Alberti *et al.*, 2001) and forest connectivity using the Aggregation Index produced by Fragstats 3.1 (McGarigal *et al.*, 2002). Once I identified a set of landscapes below 1000 m in elevation that represented a range of landcover composition and connectivity using the remotely sensed data, fieldworkers visited sites to select those that were predominately single family residential, similar in forest structure and composition, and without extensive agricultural activity.

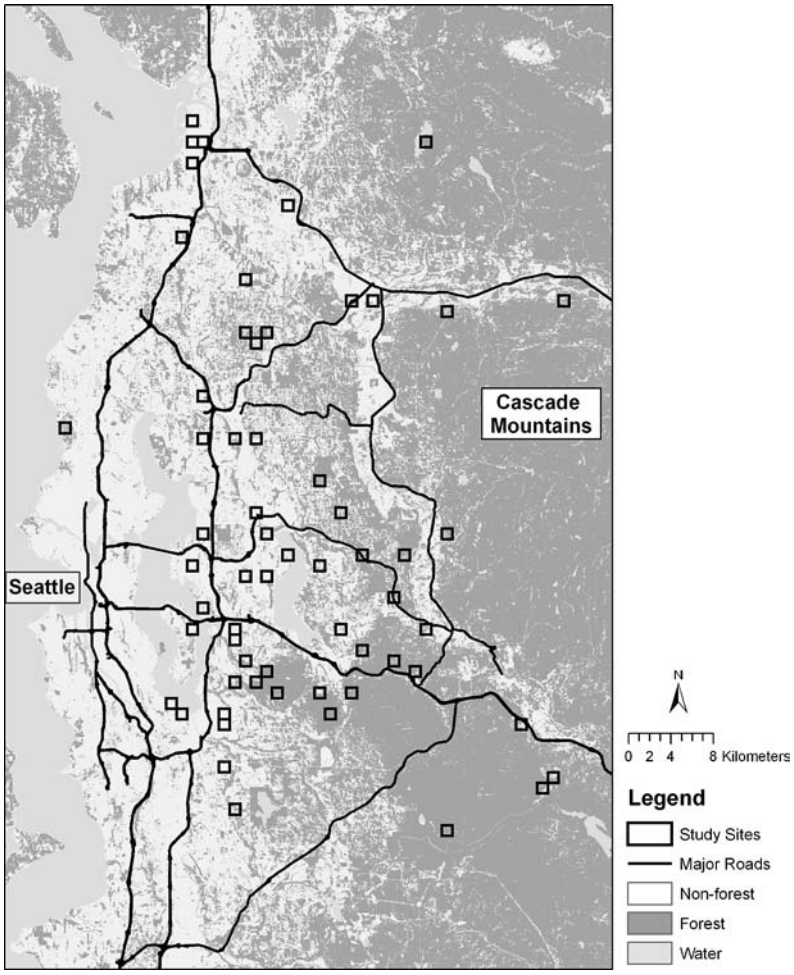

Figure 1. Map of the study area indicating forest and urban land cover, location of study sites (open squares), and size of study landscapes ($1Km^2$).

I selected landscapes to span the available range of variables in the study area. Urban landcover ranged from 4–77% with a mean (± S.E.) of 36 ± 3. Urban patch size ranged from 0–89 ha with a mean of 12 ± 3. Forest aggregation ranged from 0–0.96 with a mean of 0.70 ± 0.03. I could not include some combinations of variables, such as low percent urban landcover/high mean urban patch size, because they did not exist in the metropolitan region.

Bird surveys

Each study site was surveyed for birds in a single year (1999, 2000, 2001, or 2004; see Donnelly and Marzluff, 2004a, b for details). Measured diversity of a site increases with

additional years of study, but in the relatively species-poor bird communities of western Washington this increase is insufficient to obstruct the strong response of bird diversity to disturbances as large as urbanization. A survey consists of four visits to each site to count birds during the breeding season (roughly April to August). During each visit we recorded all birds detected in or just above the canopy by sight or sound during 10 min within a fixed area (50 m from the count location; Ralph *et al.*, 1993). We surveyed eight points within each landscape (2 in forest fragments and 6 in settlements) during each of our four visits. All points were in forest at our seven forested reserve sites. We allocated more effort to settlement than forest because a previous study in the same region indicated that birds and vegetation were more variable in settlements (Donnelly, 2002). All points were >150 m apart, with the exception of a few forest points where we maximized separation within the only forest fragment that existed on the landscape. We did not conduct more than four surveys per landscape because <2 new species are detected in forests with increased effort (Donnelly, 2002). We did not consider migrant birds that did not breed in our study area, birds that bred primarily in riparian corridors, birds that bred in low density below 1000m, or birds that ranged over large areas because our survey technique was unable to assess how these birds were using the field sites.

Surveyed birds were classified into three guilds (Table 1). Native forest birds ($n = 19$) were those routinely found in large, second growth, coniferous forests in the region. Synanthropic birds ($n = 9$) were those dependent on human settlement (Johnston, 2001). Early successional species ($n = 30$) were a diverse suite of birds that are found in greatest abundance in meadows, fields, edges, young forests, and deciduous, riparian woodlands.

Statistical analyses

I completed all statistical analyses using the Statistical Package for Social Sciences 10.1.3 (2001), except non-linear regression where I used Sigma Plot 8.0. To meet the assumptions of parametric tests, I transformed percentages (arcsine square root) prior to analysis.

Results

Empirical bird diversity in Seattle

The number of bird species in a 1 km^2 landscape comprised of single family housing and fragments of native coniferous forest was strongly correlated with the percentage of native forest (figure 2). This was not a linear relationship, but a significantly quadratic one (Richness = 18.1 + 43.6 (%forest) −41.2 (%forest)^2; $F_{2,60} = 19.8$, $P < 0.0001$). Over a third of the variation in bird species richness was accounted for by this relationship ($R^2_{\text{adjusted}} = 38.5\%$). Richness peaked at 50–60% forest in the landscape.

Bird species richness is determined by the balance between retention of native forest birds and the gain of synanthropic and early successional species (figure 3). Loss of native forest birds was linearly related to loss of forest ($R^2_{\text{adjusted}} = 53.8$; $F_{1,60} = 70.9$; $P < 0.0001$). Colonization of synanthropic species declined quadradically with gain in forest ($R^2_{\text{adjusted}} = 63.1$; $F_{2,60} = 52.3$; $P < 0.0001$). Colonization of early successional species peaked

Table 1. Songbirds surveyed in the urbanizing landscapes in and around Seattle, WA, USA categorized into three guilds relevant to urban ecosystems. Native forest species are routinely found in the mature, second growth, coniferous forests that form the natural vegetative matrix of the region. Syanthropic species obtain critical resources from humans and are common inhabitants of human settlements. Early successional species are native species that are rare in mature coniferous forests, but common in fields, meadows, regenerating forests, edges, grasslands, ponds, and deciduous, riparian areas

Native forest	Synanthropic	Early successional
American robin	American crow	American goldfinch
Turdus migratorius	*Corvus brachyrhynchos*	*Carduelis tristis*
Black-throated gray warbler	Anna's hummingbird	Band-tailed pigeon
Dendroica nigrescens	*Calypte anna*	*Columba fasciata*
Brown creeper	Barn swallow	Bank swallow
Certhia americana	*Hirundo rustica*	*Riparia riparia*
Chestnut-backed chickadee	Brewer's blackbird	Bewick's wren
Poecile rufescens	*Euphagus cyanocephalus*	*Thryomanes bewickii*
Dark-eyed junco	Brown-headed cowbird	Black-capped chickadee
Junco hyemalis	*Molothrus ater*	*Poecile atricapillus*
Downy woodpecker	European starling	Black-headed grosbeak
Picoides pubescens	*Sturnus vulgaris*	*Pheucticus melanocephalus*
Golden-crowned kinglet	House finch	Bushtit
Regulus satrapa	*Carpodacus mexicanus*	*Psaltriparus minimus*
Hairy woodpecker	House sparrow	Cassin's vireo
Picoides villosus	*Passer domesticus*	*Vireo cassinii*
Hammond's flycatcher	Rock pigeon	Cedar waxwing
Empidonax hammondii	*Columba livia*	*Bombycilla cedrorum*
Hermit thrush		Common yellowthroat
Catharus guttatus		*Geothlypis trichas*
Hutton's vireo		Killdeer
Vireo huttoni		*Charadrius vociferus*
Pacific-slope flycatcher		MacGillivray's warbler
Empidonax difficilis		*Oporornis tolmiei*
Red-breasted nuthatch		Northern flicker
Sitta canadensis		*Colaptes auratus*
Spotted towhee		Olive-sided flycatcher
Pipilo maculatus		*Contopus cooperi*
Steller's jay		Orange-crowned warbler
Cyanocitta stelleri		*Vermivora celata*
Swainson's thrush		Pine siskin
Catharus ustulatus		*Carduelis pinus*

(*Continued on next page*)

Table 1. (*Continued*)

Native forest	Synanthropic	Early successional
Western tanager		Purple finch
Piranga ludoviciana		*Carpodacus purpureus*
Wilson's warbler		Red crossbill
Wilsonia pusilla		*Loxia curvirostra*
Winter wren		Red-winged blackbird
Troglodytes troglodytes		*Agelaius phoeniceus*
		Northern Rough-winged swallow
		Stelgidopteryx serripennis
		Rufous hummingbird
		Selasphorus rufus
		Savannah sparrow
		Passerculus sandwichensis
		Song sparrow
		Melospize melodia
		Tree swallow
		Tachycineta bicolor
		Violet-green swallow
		Tachycineta thalassina
		Warbling vireo
		Vireo gilvus
		White-crowned sparrow
		Zonotrichia leucophrys
		Western wood pewee
		Contopus sordidulus
		Willow flycatcher
		Empidonax traillii
		Yellow-rumped warbler
		Dendroica coronata

in landscapes with 50–60% forest ($R^2_{\text{adjusted}} = 48.4$; $F_{2,60} = 29.1$; $P < 0.0001$). Thus, bird communities in landscapes 50 – 60% forest have high species diversity because they support rich mixes of native forest birds, early successional species that use grasslands and forest openings, and synanthropic species that benefit from people. Bird communities in more urban areas are impoverished because only about eight synanthropic species and fewer than five native species exist in mostly paved landscapes. Likewise, communities in mostly forested areas are impoverished because they are composed nearly entirely of 15 native forest birds.

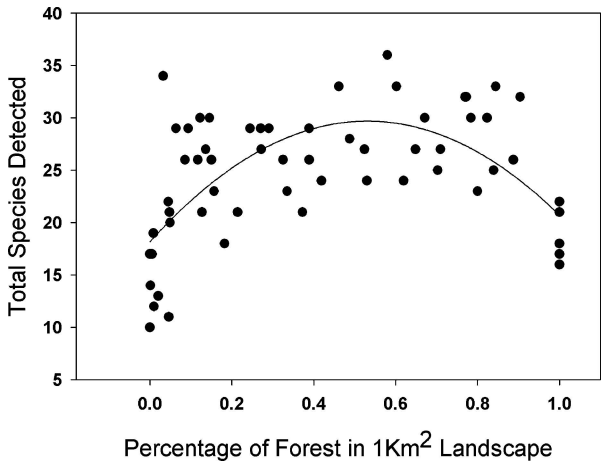

Figure 2. Change in avian diversity with progressively less settlement (more forest). Each point is a study site; control sites ($n = 7$) have 100% forest in their landscapes.

Colonization of suburbs by early successional species, most of which are native to the region (Table 1), appears most influential to the relationship between bird diversity and human settlement (figure 4). The gain in early successional species, and to a lesser extent synanthropic species, exceeded the loss of native forest species at all sites where forest cover was between 20 and 90% (figure 5). Extinction outpaced colonization at the most urban and most wildland (forested) sites.

Development of a general theory

Extinction and colonization of human settlements by mobile species like birds appears to vary with the proportion of natural vegetation remaining in the landscape. Moreover, colonization can be different for synanthropic species and native species characteristic of seral stages created or simulated by settlement. Diversity at any point along a gradient of urbanization, represented in my model by the amount of natural vegetation in a landscape, therefore equals:

$$(C_{\text{syn}} + C_{\text{ser}}) - E,$$

where, C_{syn} is the number of synanthropic species colonizing the landscape, C_{ser} is the number of species colonizing the landscape from newly created seral stages, and E is extinction of native seral stage species from the landscape.

Here I consider some possible relationships between extinction, colonization, and the amount of remaining natural vegetation in an attempt to pose testable hypotheses useful in future investigations of biological diversity in urbanizing landscapes.

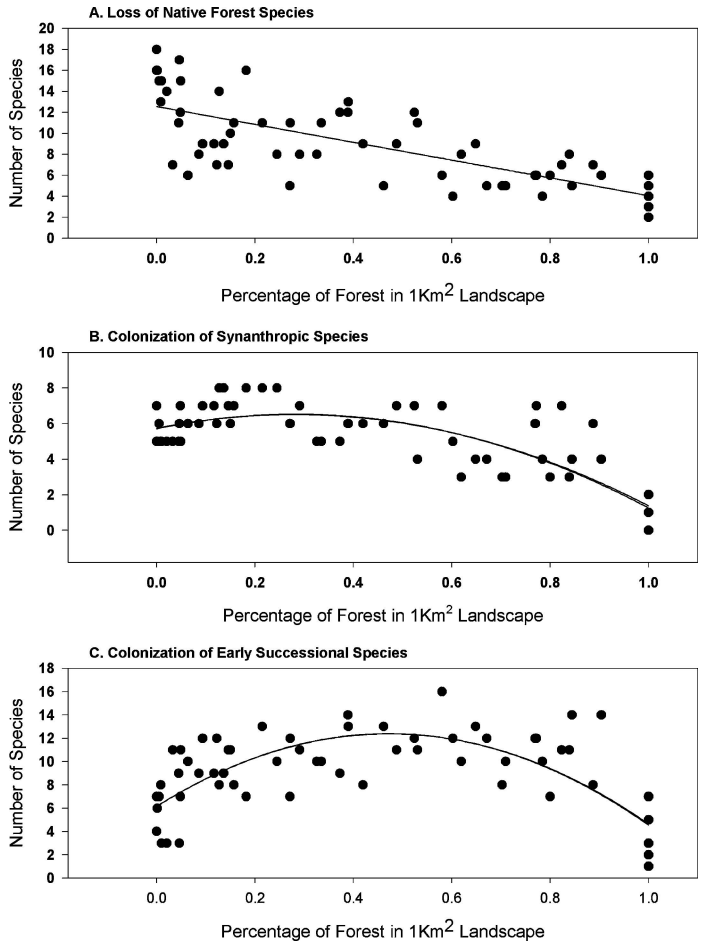

Figure 3. Reponses of three guilds of birds to reductions in settlement (increased forest). Individual species in each guild are listed in Table 1.

Extinction will certainly increase as more native vegetation is replaced by settlement, but the form of this relationship and magnitude of the loss may vary with aspects of the remaining vegetation. Consideration of the variation in human use and the arrangement of the natural vegetation that remains (figure 6(A)) suggest two testable hypotheses:

(1) Where remaining natural vegetation is widely scattered and large patches are rare, extinction rates should be higher and rise more sharply with urbanization than where remaining vegetation includes some large or connected patches (Shafer, 1999; Donnelly and Marzluff, 2004a).
(2) Where human use of remaining natural areas for recreation, resource extraction, or other purposes that introduce exotic plants and animals, simplify structural complexity,

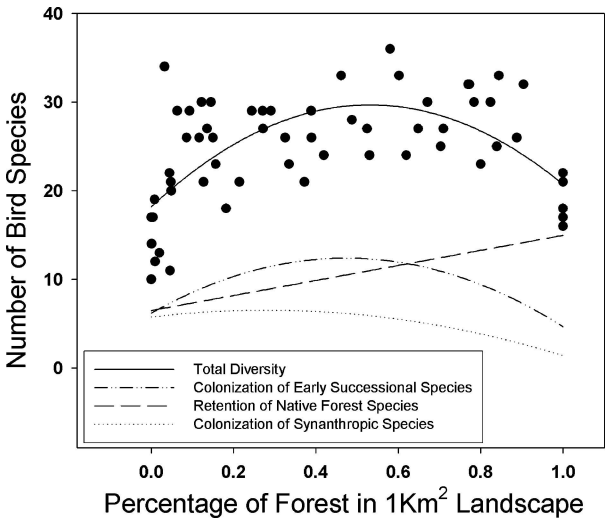

Figure 4. Influence of three guilds of birds on total avian diversity. Solid curve and points are the change in diversity from figure 2. Dashed and dotted lines represent three guilds and can be summed to equal the total diversity at any point on the gradient of urbanization (amount of forest).

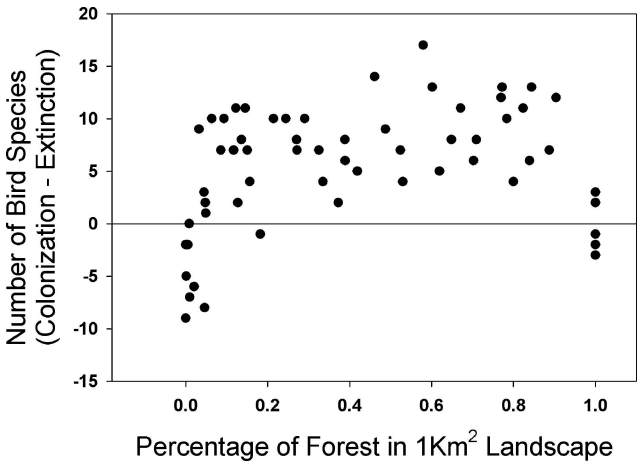

Figure 5. Difference in the amount of colonization by synanthropic and early successional species and extinction of native forest birds in communities as a function of settlement (reduction in forest). Values above the horizontal line indicate that colonization was greater than extinction. Values below the horizontal line indicate that extinction was greater than colonization.

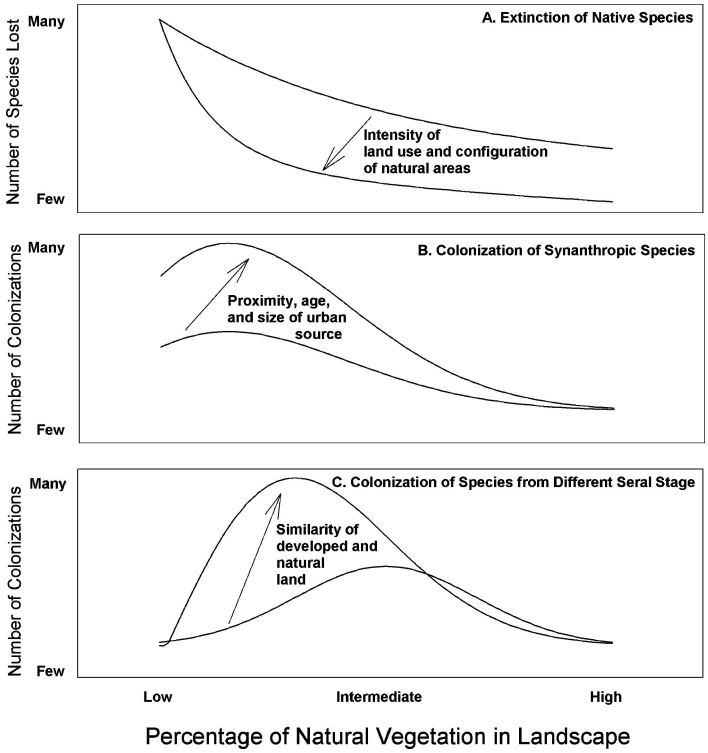

Figure 6. Hypothesized variation in extinction and colonization as a function of urbanization (loss of forest cover).

reduce shrub and ground cover, or reduce the area's productivity, extinction should rise sharply with urbanization regardless of how the natural areas are configured.

Colonization curves may take a variety of shapes with respect to the occurrence of natural vegetation in a landscape, but certainly they will generally decline with reduced land cover change (i.e., a high percentage of native vegetation in the landscape; figure 6(B) and (C)). In Seattle, colonization was aided by the use of interspersed built and unbuilt areas by black-capped chickadees, downy woodpeckers, and red-breasted nuthatches, and by the abilities of violet-green swallows to find, exploit, and pack into subdivisions where the forest canopy was perforated by houses. This leads me to four hypotheses:

(3) Where colonizing species benefit from edge and habitat, colonization will peak at intermediate levels of land cover change.
(4) Where colonizing species benefit from release from predators or competitors sensitive to human activity, colonization will peak in mostly urban landscapes.

(5) Where colonists have high dispersal abilities and are able to use small habitat patches, colonization will also peak at intermediate levels of land conversion (figure 6(C)).
(6) Colonization by synanthropic species will be proportional to the amount, proximity, and age of settlement (figure 6(B)).

The pattern of diversity with respect to the amount of urbanization is determined by the difference in colonization and extinction. Colonization should strongly influence the pattern if it exceeds extinction. This was the case in my empirical example, probably because many synanthropic and early successional colonists were nearby. However, in landscapes with frequent extinctions and rich native faunas, the shape of the extinction curve is expected to exert a strong influence on the pattern of diversity with respect to urbanization. Four hypotheses are testable:

(7) Colonization will determine the pattern of diversity with respect to urbanization where urban areas provide rich, large, and proximal pools of synanthropic colonists (figure 6B).
(8) Colonization will determine the pattern of diversity with respect to urbanization where land transformation creates seral stages that are very dissimilar from existing natural vegetation. Dissimilarity between the natural and built environments will allow native species not normally found in the existing natural landscape to colonize urbanizing landscapes (figure 6(C)).
(9) Extinction will determine the pattern of diversity with respect to urbanization where extinction exceeds colonization. The resulting pattern of diversity should follow the shape of the extinction curve in direct proportion to the magnitude of extinction relative to colonization.
(10) Where extinction is substantial, it may also balance colonization at each point along the gradient of urbanization leading to a constant value of diversity regardless of the amount of urbanization. In this case, turnover in species composition is expected despite constancy in species diversity.

The preceding theory and predictions are concerned with local, or alpha, diversity. Regional and global diversity will also respond to urbanization, primarily through the process of biotic homogenization (Olden *et al.*, 2003). Homogenization, or the reduction in regional and global diversity as cosmopolitan exotic species invade and eventually replace native endemic species, is thought to depend primarily on the type and number of invasive and native species, the historical similarity among donor and recipient communities, and the richness of recipient communities (Olden and Poff, 2003). Considering biotic homogenization in urbanizing landscapes from the colonization and extinction perspective I have detailed above provides three hypotheses:

(11) The cosmopolitan nature of synanthropic species will determine the degree of homogenization observed in urban plant and animal communities. Where most synanthropic

colonists are from the region of study, homogenization will be less than where synanthropic colonists occur globally in association with humans.

(12) The relative importance of synanthropic versus seral stage colonists will determine the degree of homogenization in urban plant and animal communities. Because most seral stage colonists are native to the locale or region, where they colonize more frequently than cosmopolitan, synanthropic species, homogenization of regional (and especially global) urban communities will be slow.

(13) The degree of homogenization in urban plant and animal communities will be greatest when colonization precipitates extinction, for example when colonists prey on or compete with remaining native species.

Discussion

The diversity of birds in small landscapes (1 Km^2) varied with the amount of natural vegetation, and its converse, the amount of urban land cover. Landscapes with intermediate amounts of settlement and forest cover had the greatest diversity; 20–35 species of songbirds. In contrast, most landscapes with either extensive settlement or no settlement had fewer than 20 species of songbirds. Low diversity in the most natural landscapes was consistent, but at first perplexing. All seven reserves had low bird diversity that appeared to reflect the relatively homogeneous, coniferous forest. Among the seven reserves, those that had the most diverse land covers (riparian, regenerating forests) also had the greatest bird diversity. But even these sites only had a maximum diversity of 22 species; well below that found in moderately settled areas. The correlation between urbanization and bird diversity has biological, theoretical, and practical implications.

Biological implications

The response of bird diversity to the disturbance of settlement is generally consistent with the intermediate disturbance hypothesis (Roxburgh *et al.*, 2004), and specifically consistent with the disturbance heterogeneity model (Porter *et al.*, 2001). Where disturbance is extreme, syanthropic species dominate bird communities. Where disturbance is rare, native forest species dominate. But where disturbance is intermediate, a rich diversity of species coexist. Determining the factors allowing for such coexistance has motivated ecologists for five decades (Roxburgh *et al.*, 2004). In the urbanizing region around Seattle, intermediate disturbance increases local bird diversity most clearly by increasing the local diversity of resources, confirming Porter *et al.*'s (2001) extension of the disturbance heterogeneity model to urban ecosystems. As expected, diversity peaked where the novel urban land cover occupied approximately 50% of the landscape. Settlement of this principally forested region produces edges, grasslands, small ponds, canopy breaks, gardens, anthropogenic nest sites, and deciduous woodlands that are rapidly colonized by species rarely found in pure coniferous forests of the Pacific Northwest. Intermediate disturbance combines rich mixes of land covers into small areas, each of which is inhabited by a unique set of birds. Birds characteristic of built and early successional landscapes invaded the formerly continuous

coniferous forest to increase diversity. In a similar way, urbanization increased tree species diversity, which together with increased landscape patchiness accounted for increased bird diversity in moderately-settled suburban areas of California and Ohio (Blair, 2004).

Settlement does not appear to stymie the superior competitive abilities of some species, and therefore does not appear to alleviate competitive exclusion as may occur in some intermediately disturbed systems (Connell, 1978; Huston, 1979). In fact, settlement may increase competitive interactions within a locally diverse community. Urbanization in Seattle adds a second wren (Bewick's wren), several titmice (bushtit, black-capped chickadee), a host of aerial insectivores (swallows and flycatchers), a versatile ground forager (song sparrow), and many seed eaters which could compete with native forest winter wrens, Pacific-slope and Hammond's flycatchers, spotted towhees, and chestnut-backed chickadees. I have no evidence of this, but my study is limited by the relative newness of European settlement in the western United States.

The characteristics of colonizing species suggests that biotic homogenization will be slow and may be confined to regional, rather than global scales. Cities in the coniferous forests that flank the northern Pacific Ocean are likely to develop similar avifaunas as a few cosmopolitan, synanthropic species (European starling, rock pigeon, American crow, house finch, and house sparrow) and a diverse collection of early seral stage, regional natives invade human settlements. While this new collection of species will be similar among cities in the region, this is not unnatural. Pacific coniferous forests have similar avifaunas because they have few locally endemic birds. Regional homogenization is unlikely to cross natural boundaries because nearby mountain, dry forest, shrubland, or grassland cities would each attract a distinct set of early seral stage colonists. The sort of invasion of urban bird communities I documented is unlikely to produce rapid and global homogenization because few globally-distributed species occurred and these did not directly cause the extinction of native species. House sparrows and rock pigeons do not appear to compete with native sparrows and pigeons, although they may increase the susceptibility of native species to exotic diseases. European starlings have minimal effects on native cavity nesters (Blewett and Marzluff, 2005).

Seattle is a young city, barely 100 years old. Most of my study areas are in the region where development is rapidly occurring and has only been occurring for a few decades. Therefore, persistence of high diversity where disturbance is intermediate and maintenance of heterogeneous avifaunas may not be stable in ecological time (e.g., over tens of bird generations). In fact, we can already detect some relaxation of diversity in intermediately-disturbed subdivisions that vary in age from 20 to 100 years (Donnelly 2002; Ianni and Marzluff, in preparation). However, relaxation of diversity is not sufficient to erase the peak in diversity seen in moderately settled landscapes. It appears that, in the variable geography of the Pacific Northwest, heightened bird diversity in moderately urbanized locales does not warn of impending collapse of diversity as it does in many fish communities (Scott and Helfman, 2001). I suspect urban bird diversity will remain high in the Pacific Northwest because invading synanthropic species offer little competition to native species. If current processes remain in operation, then bird communities should remain diverse, but differ in composition from historical communities as settled forests change in quality, age, and perhaps predator loads. Changing bird communities remain effective early warning systems,

alerting people to the consequences of their actions. But, unlike plants and animals facing severe competition or predation from invading species (e.g., Scott and Helfman, 2001), diverse urban bird communities may alert people to the possibility of balancing their needs with the needs of other species. Achieving this requires understanding and planning (see **Practical implications**).

Other nuances of Seattle may also make my results relatively site-specific. Seattle is surrounded by expanses of natural lands that may function as important reservoirs of native forest birds. Perhaps these are sources that continually restock urban areas. As a coastal city, Seattle's climate is benign, but its northern latitude and relatively simple, coniferous forest produces a simple bird community. Perhaps richer avian assemblages, or more seasonally variable ones, will respond differently to urbanization. This has not been observed, as researchers have found moderate settlement (suburban to exurban; definitions in Marzluff *et al.*, 2001b) to increase bird diversity in a variety of areas (forests, shrublands, and grasslands from coastal, desert, and inland biomes; Sewell and Catterall, 1998; Blair, 2004; Zack Jones and Carl Bock, personal communication). But little is known about urban bird dynamics in rich tropical locales (Marzluff *et al.*, 2001b).

Ongoing research is shedding light on the mechanisms underlying extinction of native forest birds in my study area. Reproduction and dispersal do not appear to be compromised by settlement (Donnelly 2002; Donnelly and Marzluff, 2004a; Blewett and Marzluff, 2005; Kara Whittaker, unpublished data). Rather, low population size resulting from reduced amount and quality of natural forest appears to reduce long-term viability of populations (Donnelly 2002; Donnelly and Marzluff, 2004a). Reduced survival of fledged young and perhaps breeding adults may also be important.

The generally greater response of bird diversity to the type and amount of vegetation, rather than to its configuration is likely taxon-specific. Birds are exceedingly mobile which allows them to quickly recolonize small habitat patches and travel between disjunct patches. Species less able to traverse landscapes, for example aquatic insects or small mammals, may be more responsive to the pattern of urbanization (Alberti and Marzluff, 2004; Hansen *et al.* in press).

Theoretical implications

Investigating the processes of extinction and colonization separately helps to untangle the opposing forces that define an area's standing diversity. This approach has been successfully pioneered in urban settings by Blair (1996, 2001a, 2004). My expansion of these ideas into a graphical format with explicit hypotheses about factors that may affect colonization and extinction in urbanizing landscapes (figure 6) is meant to stimulate others to test, refute, and refine the ideas. One important area in need of refinement is the actual measurement of extinction and colonization. I simply determined these by an annual assessment of presence or absence. It may be better to consider a longer time span of absence before concluding extinction. Detailed study of the process of colonization is also needed. Do some colonists visit a site early in the season, but not stay? Do others use a site inconspicuously without breeding there? These refinements would aid our understanding of the dynamics of bird

diversity. Studies of extinction and colonization may be especially insightful if they can be done before, during, and after development.

The three guilds of birds I have used make sense in an urbanizing environment where settlement adds novel anthropogenic resources, produces a variety of seral stages, and removes currently natural vegetation. Further insights could come by subdividing these guilds into more traditional ones like cavity versus ground nesters or aerial versus foliage foragers. However, an even more insightful approach is to look at the colonization and extinction of individual species and relate this to land cover change resulting from urbanization. Testing for community nestedness and relating this to urban gradients is powerful (Lomolino, 1996). In my study area, this approach showed that many species have thresholds of occurrence with respect to the amount of urban or forest land cover (Donnelly, 2002; Donnelly and Marzluff, 2004a). In response to settlement, back-capped chickadees, song sparrows, American crows, black-headed grosbeaks, and bushtits are the first to colonize. Black-throated gray warblers, hairy woodpeckers, western tanagers, Pacific-slope flycatchers, brown creepers, and winter wrens are the first to disappear.

Practical implications

Planners, developers, policy makers, managers, and homeowners can use the results of ecological studies in urban environments to increase the sustainability of human settlement. Sustainable development must have at its foundation ecological sustainability. Ecological sustainability is related to diversity (Loreau, 2000), so providing for diverse bird communities in urbanizing landscapes is one step down the path to sustainability. My results suggest that, at the local scale, bird diversity is enhanced by moderate settlement. But this does not mean that moderately settling all land will enhance bird diversity regionally. Widespread settlement and globalization clearly do not enhance diversity. They homogenize and reduce it (Lockwood *et al.*, 2000; Blair, 2001b), especially as larger geographic scales are considered (Sax and Gaines, 2003). While I suspect the benign nature of invading species and geographic complexity of my study region will slow and limit homogenization, if urban planners and land managers consider the needs of native forest species, early successional species, and synanthropic species separately they can actively work against homogenization. Moderate settlement enhances diversity in my study area by providing habitats used primarily by early successional and deciduous forest birds. Synanthropic and native forest birds occur in moderately settled areas, but to provide more explicitly for them, requires maintaining some extremely developed as well as some undeveloped land. Providing for the full diversity of birds requires the full diversity of habitats—from developed to undeveloped. Simply stated, fighting homogenization and maintaining bird diversity is best accomplished by not doing the same thing everywhere (Bunnell, 1999). Planners who encourage the same style of development across a landscape may increase local diversity or favor one group of species over another, but at the regional scale they will reduce biological diversity and therefore lower the sustainability of development.

Not doing the same thing everywhere requires planning. Often in my study area developers lobby for increased settlement, while conservation activists argue for large, undisturbed reserves. If both "win", birds will suffer because few areas of moderate settlement may

Table 2. Conservation strategies for birds in urban areas and the participants who must cooperate for effective implementation. Strategies are from Donnelly (2002), Donnelly and Marzluff (2004), and Blewett and Marzluff, 2005

Strategy	Regional planner/ policy maker	Local planner/policy maker	Large-scale developer	Conservation activist	Conservation/ restoration scientist	Educator/ interpreter	Local open space manager	Builder	Home owner
Don't do the same thing everywhere	X	X	X	X	X	X	X	X	X
Create large public reserves	X	X	X				X	X	
Implement growth management	X	X	X				X	X	
Monitor land cover change	X			X	X				
Maintain/restore native vegetation	X				X	X	X		X
Demonstrate value of open space				X	X	X			
Keep interior conditions in some open space				X		X	X		X
Reduce anthropogenic food supplementation						X	X		X
Maintain snags and short-lived trees		X				X	X	X	X
Increase native shrub and ground cover							X	X	X
Encourage premium pricing for functional open space		X	X	X		X		X	X
Manage exotic predators							X		X
Educate home owners about edge effects and disturbance				X	X	X			
Create stewardship incentives	X	X		X					

remain. In terms of figure 2, we will end up with both low diversity ends of the curve on the landscape and miss the high diversity peak. Planners, policy makers, and open space managers interested in maximizing biological diversity should devise strategies and incentives to maintain moderately-settled areas in the region and balance their occurrence with undeveloped and highly developed landscapes.

Planning at the local to regional scale requires the cooperation of developers, policy makers, urban planners, homeowners, and urban ecologists. Each and every strategy that our work suggests will increase bird diversity requires actions to be carried out by a diversity of participants (Table 2). For example, activists, scientists, and educators will need to cooperate to inform residents, planners, and policy makers about relevant research like the effects of disturbance on forest birds. Likewise, builders, developers, regional planners, county commissioners, and other policy makers will need to cooperate to implement effective growth management.

Urban ecologists will increasingly be called on to share their science with planners, policy makers, developers, and homeowners. To effectively serve this varied clientele requires nontraditional training. Specifically, urban ecologists will increasingly require interdisciplinary training to understand how policies are formulated and implemented, how planners design landscapes, and what people want from their immediate surroundings. New interdisciplinary programs are emerging (Alberti *et al.* 2003, Tress *et al.* 2003), but students must open their eyes, ears, and minds widely. International travel is increasingly important. Take the window seat and look at patterns of development. Ask whether the patterns below you provide local, regional, and global diversity. Learn about foreign policies and value systems that seem to result in diverse landscapes. Help globalize knowledge so that we do not continue to do the same thing everywhere.

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