Chapter 8

POPULATION AND COMMUNITY DYNAMICS

8.1 Biodiversity, Ecosystem Function, and Resilience

The study of urban ecology must address the scientific debate on how biodiversity relates to ecosystem function, stability, and resilience (Peterson et al. 1998). Though the term biodiversity has multiple definitions and interpretations, the definition provided by Wilson (1992, 393) may best capture its essence. Wilson emphasizes "the variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families and still higher taxonomic level," as well as "the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live."

Ecological scholars disagree on the role that biodiversity plays in the functioning of ecosystems: The issue is not simply what species are involved in what specific ecosystem functions, but the importance of diversity for the functioning of ecosystems and the role that it plays in their resilience (Loreau et al. 2001). Scientists also disagree on what drives the patterns of species diversity and the nature of ecological communities. Different theories can be distinguished based on whether they see community assembly as based on niches (MacArthur 1970, Levin 1970), or dispersal (MacArthur and Wilson 1963), and whether they are neutral (treating individual species as essentially identical) (Hubbell 2001) or non-neutral (assuming that different species behave in different ways from one another) (Ehrlich and Ehrlich 1981, Walker 1992, Levin 1999). The lack of resolution on these different perspectives may simply indicate that they are all true at some level (Hubbell 2001). At the same time, they all share a biased disciplinary perspective: They fail to appreciate the mutual interactions and feedback between ecosystem function and biodiversity. These different perspectives have important implications for conservation, and for efforts to integrate humans into ecological thinking.

Despite these differences, however, a consensus on important aspects on the relationship between biodiversity and ecosystem function is emerging

(Hooper et al. 2005). During the past decade, the debate has shifted its focus from number of species to functional groups and underlying mechanisms (Grime 1997, Loreau et al. 2001, Srivastava and Vellend 2005). Scholars have pointed out the need to formulate new hypotheses, and to formally test theories and models that integrate community ecology and ecosystem science in a unified framework (Loreau et al. 2001). Yet the debate has not fully integrated humans or effectively explored how their inclusion might change our understanding of the relationship between biodiversity and ecosystem function. Building on current advances, in this chapter I focus on how urbanization patterns may affect the relationship between biodiversity, ecosystem processes, and resilience, and the implications for robust generalizations in human-dominated ecosystems. I ask how humans affect both the relationship between biodiversity and ecosystem processes, and the role of biodiversity in the stability of ecosystems. I conclude the chapter with an empirical exploration of bird diversity and human disturbance on an urban-to-rural gradient.

Species richness and ecosystem function

Ecological studies have provided ample evidence that different species perform diverse ecological functions within the systems they inhabit; for example, they cycle nutrients, regulate trophic mechanisms, pollinate plants, disperse seeds, and control natural disturbance (Hooper et al. 2005). Thus a change in species composition may imply predictable functional shifts when sets of species with certain traits are replaced by sets with different traits (Grime et al. 2000, Loreau 2001). Substantial evidence shows that functional diversity depends on species richness—but to what extent does species richness affect stability (Tilman et al. 1996)? Scientists disagree about the relative influence of functional substitutions and species diversity on ecosystem functioning (Loreau 2001). Furthermore, we do not know whether and to what extent their relative importance changes under changing conditions. Understanding the relationship between species diversity and ecosystem function becomes even more relevant in the context of increasing human-induced impact due to land cover change and urbanization (Hooper et al. 2005).

If changes in species composition affect the efficiency with which resources are processed within an ecosystem, we would expect that species richness would affect ecosystem function. But much is still unknown about the ways ecosystems respond to changes in species richness. Several competing models were initially proposed to describe this dynamic (Figure 8.1, Naeem et al. 2002). The null hypothesis states that species richness has no effect on ecosystem functions (Vitousek and Hooper 1993). Considerable

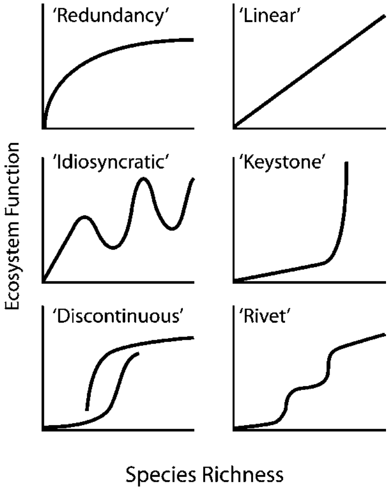

Figure 8.1. Alternative models of species richness and ecosystem function. The graphs represent competing hypotheses regarding the relationship between species richness and ecosystem function—that is, the ecological role that species diversity plays (Naeem et al. 2002, p. 5).

evidence contradicts this hypothesis, however, leading to several alternative hypotheses. The *rivet* and *redundancy* hypotheses suggest that certain species may drive the functioning of an ecosystem, while others have various impacts on the way those functions occur. The rivet hypothesis (Ehrlich and Ehrlich, 1981) suggests that ecosystems are like plane wings: Ecosystem functioning (the plane) may or may not be compromised depending upon which species (rivets) are lost. A plane can lose several rivets before a wing falls off. The ecological functions of different species overlap; therefore, even if a species dies out, the system's ecological functions may persist because other species that perform similar functions can compensate for the lost one.

The redundancy hypothesis is based on a concept similar to the "rivet hypothesis." (Ehrlich and Ehrlich 1981) In addition, it advances that conservation efforts should focus on the species that uniquely represent a given functional type, because of their role in maintaining ecosystem integrity. This hypothesis assumes that above a critical level most species are functionally redundant. The *idiosyncratic* hypothesis emphasizes that the change in ecosystem functioning associated with changes in species diversity is unpredictable because individual species have such complex and diverse roles (Lawton 1994). Under the *keystone* hypothesis, ecosystem function declines rapidly with the loss of species that are crucial to mediating such functions, and diversity is consequently reduced below its natural levels (Walker 1992).

However, these early hypotheses only partially address the complex relationship between biodiversity and stability. During the past decade, important advances have occurred in the debate as observational, experimental, and theoretical studies have helped researchers to better articulate the scientific questions. Recent studies suggest that biodiversity may provide "insurance" or a buffer to maintain ecosystem function in the presence of environmental variability since different species respond differently to environmental fluctuations. Furthermore, scholars recognize that, given the lack of explicit definitions, the debate has not always been productive, which leads to the current scientific controversy (Pimm 1991). And that debate is still influenced by an old paradigm of stability (Loreau et al. 2001). Loreau et al. (2001) point out that the concept of "stability" refers to several properties whose relationships with diversity may change across levels of organization; more importantly, that stability has been approached mainly within a deterministic, equilibrium theoretical framework. Different concepts of stability produce a different diversity-stability relationship (Ives and Carpenter 2007).

The evidence that diversity matters to the functioning of ecosystems is growing. Cardinale et al. (2006) conducted a meta-analysis of 111 studies on the effects that species diversity has on the functioning of numerous trophic groups in multiple types of ecosystems. They found consistent patterns across different trophic groups (producers, herbivores, detritivores and predators) and ecosystem types (aquatic and terrestrial). They conclude that species loss does indeed affect ecosystem functioning (i.e., abundance or biomass of the focal trophic group), but the magnitude of these effects is determined by species identity.

More recently, researchers have started to shift their focus from the number of species to the mechanisms by which biodiversity affects ecosystem function (Loreau et al. 2001). They have started to focus on functional groups, exploring the extent to which functional substitutions alter a variety of ecosystem properties such as productivity, decomposition rates, nutrient cycling, as well as their stability and resilience. Findings indicate that diversity is essential to sustain the functioning of ecosystems undergoing change (Schläpfer and Schmid 1999, Loreau 2000). However, current studies cannot determine whether the effect is due to a few key species or the diversity of species. Current explorations of the mechanisms that link biodiversity and ecosystem function are focusing on two major aspects: (1) deterministic processes, such as niche differentiation and facilitation, which lead to "complementarity" and (2) stochastic processes involved in community assembly, where random sampling coupled with local dominance of highly productive species, can also lead to increased primary production and diversity (Loreau et al. 2001).

If the effects of humans are brought into the picture, a mechanistic approach could help expand our understanding of ecosystem dynamics in urbanizing regions and guide ecosystem management strategies. But to fully appreciate the implications of including humans in such a framework, we need to consider several levels of human interactions with biodiversity and ecosystem function. The first level involves the influence of humans in community assembly. The second is the influence that human settlements have on the species-area relationship. The third is the way that stability domains change in the presence of humans.

Humans can affect species composition and their functional roles in ecosystems both directly by reducing the overall number of species or by selectively determining phenotypic trait diversity. Since individual species may control community- and ecosystem-level processes (Paine 1984, Lawton 1994, Power et al. 1996), ecosystem processes may be highly affected by diversity, since changing diversity affects the probability of occurrence of these species among potential colonists (Tilman 1999, Cardinale et al. 2000). Humans can influence ecosystem processes by both altering the dominance of species with particular traits, and facilitating or impeding complementarity among species with different traits. Furthermore, human activities can influence the sampling effect by selectively reducing or increasing the pool of species representing particular functional traits.

Humans can affect species composition and their functional roles in ecosystems both directly, by reducing the overall number of species, or indirectly, by selectively determining phenotypic trait diversity. Individual species may control processes at both the community and ecosystem levels (Paine 1984, Lawton 1994, Power et al. 1996), so diversity may have a strong effect on those processes, because changes in diversity affect the probability that these species will occur among potential colonists (Tilman 1999, Cardinale et al. 2000). In addition to altering the dominance of species with particular traits, humans affect diversity by facilitating or impeding complementarity among species with different traits. Furthermore, human activities can influence the sampling effect by selectively reducing or increasing the pool of species representing particular functional traits.

Loreau et al. (2001) point out that complementarity and sampling effects can occur simultaneously, since communities with more species have a higher chance of containing a greater diversity of phenotypic traits. Rather than alternative mechanisms, there is increasing evidence that they can represent end points on a continuum from dominance of species with certain traits to complementarity of species with different traits, with intermediate scenarios, where bias in community assembly may lead to correlations between diversity and community composition that involve both dominance and complementarity (Loreau et al. 2001).

As we explore the relationship between biodiversity and ecosystem function in human-dominated ecosystems, it becomes evident that humans influence both ecosystem function and the pattern of biodiversity, as well as the relationship between them. Mutual interactions and feedback occur among biodiversity changes, ecosystem function, and abiotic factors. Humans influence all of these factors by strengthening or loosening some of these interactions and feedback loops and by creating unprecedented interactions between biodiversity and ecosystem function. Thus diversity-stability relationships cannot be understood outside the context of these complex interactions (Ives and Carpenter 2007).

When studying the impact of humans on biodiversity and ecosystem function, it is critical to acknowledge that processes influencing diversity operate at different spatial and temporal scales (MacArthur 1969, Tilman and Pacala 1993). At the local scale, dominant constraints are resource abundance, competition, predation, and disturbance. At larger scales, processes such as emigration, large-scale disturbances, and evolution operate (MacArthur 1969). Humans influence these dynamic interactions across a wide range of spatial and temporal scales through urbanization and land cover change. Recent studies have pointed out that there may be important feedback mechanisms that link ecosystem function and biodiversity across scales. Diversity is correlated with productivity directly and through several factors that influence productivity at a large scale (i.e., climate and disturbance regime). But species diversity and composition also have local effect on productivity. Potential interactions between human settlement and community assembly can be mediated by human effects on environmental processes at the local and regional scales.

Integrating humans into the study of biodiversity could also reconcile key theoretical concepts. Theories of both niche and dispersal-based community assembly can benefit by including humans. Hutchinson (1957) transformed and solidified the niche concept, changing it from a mere description of an organism's functional place in nature (Elton 1927) to a mathematically rigorous *n*-dimensional hypervolume that could be treated analytically. Hutchinson's "realized niche" included only those places where an organism's physiological tolerances were not exceeded (its "fundamental" niche) and where its occurrence was not preempted by competitors. In addition to competition, other potentially important community organizing forces, such as predation, resource variability, and human domination, are altered as a function of human-mediated dynamics. Through all these mechanisms, humans force population-level ecological functions that structure communities.

By integrating humans into the study of processes controlling biological diversity, ecological scholars may be able to resolve important puzzles in island biogeography and explain empirical results regarding the balance between colonization and extinction in human-dominated ecosystems (Marzluff 2005). The balance between extinction and colonization still regulates diversity in a human-dominated world, but as Marzluff (2005) points out: Both colonization and extinction are affected by direct and indirect human actions, including land cover change and the introduction of non-native species. As humans urbanize, they cause the emergence of new selective forces including new habitats, disturbance regimes, predators, competitors, and diseases that may drive native species to extinction (Sax and Gaines 2003, Kuhn et al. 2004, Olden and Poff 2004).

Environmental variability

An emerging paradigm in ecosystem ecology holds that there may be no single, generalizable relationship between species diversity and ecosystem function; instead, it may depend highly on context (Chapin et al. 1998, Cardinale et al. 2000). Cardinale et al. (2000) show that environmental variability (both spatial and temporal) can change both the form and cause of the relationship between diversity and ecosystem productivity. That context is important was recognized earlier (Risser 1995, Chapin et al. 1998), but only recently scholars have started to study it systematically (Cardinale et al. 2000). In addition, ecological scholars now realize that several aspects of community structure associated with species richness may control the biodiversity-ecosystem function relationship (Naeem et al. 2000, Wilsey and Potvin 2000, Cardinale and Palmer 2002). Several scholars have proposed that community structure may in fact mediate the effects of species richness on ecological processes and thus play an important role in the relationship between species richness and ecosystem function—because the same drivers of community structure might simultaneously affect that relationship (Naeem et al. 2000, Wilsey and Potvin 2000, Cardinale and Palmer 2002). Furthermore, Mulder et al. (1999) and Cardinale et al. (2002) have shown that interspecific interactions between different functional groups of organisms control the effects of species richness on ecosystem function. They hypothesize that diversity affects the efficiency and productivity of ecosystems through facilitation between species.

Environmental context and variability (in space and time) are essential elements defining the current debate on diversity and ecosystem function since variability can greatly influence the partitioning of resources among species in a system. If community structure has the potential to mediate the relationship between species richness and ecosystem function, ecological factors regulating interspecific interactions may also impact such a relationship (Cardinale et al. 2002). Disturbance can introduce variability through mechanisms such as preventing competitive dominance or introducing new potential niches. Cardinale et al. (2000) show how disturbance regimes (e.g., fires, floods, predation, etc.) might affect such relationships by regulating community structure, for example by controlling changes in the relative abundance of species and promoting species coexistence (Paine 1966, Poff et al. 1997). The *intermediate disturbance* hypothesis suggests that biodiversity is highest at intermediate levels of disturbance by precluding competitive dominance, while too much disturbance results in local extinctions (Connell 1978). Spatial heterogeneity may also increase niche diversity and enhance coexistence at the intermediate level of disturbance (Kolasa and Pickett 1991).

Species-area relationships

Within the debate on biodiversity, another area of contention focuses on species-area relationships: the idea that the number of species increases with the size of the sampling area such that larger areas will contain more species (Arrhenius 1921). This relationship is important for both ecosystem science and management. It is the basis for adequately sampling the species in a particular community, characterizing the community structure, and estimating species richness (Connor and McCoy 1979). For conservation biology, it also provides guiding principles to define the optimal size of reserves (He and Legendre 1996). Urbanizing landscapes provide unique opportunities to expand our understanding of the species-area relationship and to apply the knowledge to better design and manage urban regions.

Several hypotheses have been developed to explain species-area relationships (McGuinness 1984). The simplest is the *random placement* hypothesis (Arrhenius 1921, Coleman 1981): If individuals are randomly distributed, larger samples will contain more species. The *equilibrium* hypothesis (Preston 1960, MacArthur and Wilson 1963, 1967) explains the species-area relationship as a result of a dynamic equilibrium between colonization and extinction, which are determined by the size and isolation of islands. Island biogeography sees remnants as target areas for colonizing organisms. Larger islands support larger populations and large populations are less likely to become extinct than smaller populations. The hypothesis is that extinction rates are negatively correlated with population size due to demographic, genetic, and environmental stochasticity (Harrison 1991).

The *habitat heterogeneity* hypothesis (Williams 1964, Connor and McCoy 1979) maintains that larger areas have greater species diversity because they are more likely to encompass more diverse habitats. Islands of the same size are expected to vary in species diversity because they show different degrees of heterogeneity (McGuinness 1984). More heterogeneous areas are likely to support more species because of variations in climate, soil, topography, and other environmental factors (Williams 1943).

The *intermediate disturbance* hypothesis explains the species-area relationship as a function of variability in disturbance. The hypothesis holds that island size is related to frequency of disturbance. Small areas favor species that can tolerate more frequent disturbance, while the less frequently disturbed large areas are dominated by a few species that most efficiently exploit the resources and out-compete other species. The hypothesis thus contends that intermediate-sized areas support more species because they can support both types of species. This is described as a "humped" distribution (McGuinness 1984).

Diversity and resilience

The idea that biodiversity provides a buffer or "insurance" against major change in ecosystem function given changing conditions and environmental fluctuations is based on the assumption that separate species utilize separate niches, responding differently to future events. More diverse ecosystems offer more options than simpler ones when placed under stress. Tilman (1996) shows less extreme year-to-year fluctuations in above-ground biomass in more diverse grassland communities, and faster recovery after drought. Under the insurance hypothesis, redundancy of species is a relative concept, depending on time and circumstances.

In theory, redundancy may very well allow for substitution when species belonging to a functional group are lost. This is the foundation of the biodiversity "insurance" hypothesis. Different theories about the apparent redundancy of species, the role of keystone species, and their relationships to ecosystem function have important implications for the strategies available for preventing loss of ecosystem function. But studies have not provided sufficient evidence to resolve the scientific controversy and provide clear policy guidelines (Johnson et al. 1996, Pimm 1991).

The scale at which species perform different ecosystem function may be a key to understanding the relationship between ecosystem function and diversity. Peterson et al. (1998) points out that while most models assume that ecological functions of various species remain the same at various scales, empirical evidence tells us that different species perform these functions at specific spatial and temporal scales (Holling 1992, Peterson et al.

1998). A few key processes regulate ecosystem structures and dynamics and they can be differentiated according to temporal and spatial scales (Levin 1992, Holling 1992). Holling (1992) describes the landscape as a hierarchical structure (Holling 1992). At the finer and fastest scales—centimeters to tens of meters and days to decades—are the biophysical processes that control plant growth and form. At the largest and slower scale —hundreds to thousands of kilometers and centuries to millennia—are geomorphological processes that control topography and soils. Disturbances such as fires, storms, and insect outbreaks operate at the mesoscale.

Peterson et al. (1998) hypothesize that if the species in a functional group operate at different scales, they mutually reinforce the resilience of a function—and minimize competition among species within the group. The presence of different functional groups within a scale and the replication of function across scales provide robust ecological functioning (Peterson et al. 1998). Ecological function is supported by scale-specific processes and structures that different species utilize differently, depending upon the time and spatial scales at which they operate (Morse et al. 1985, O'Neill et al. 1991, Peterson et al. 1998). Species may share the same area but, since they operate at different times and spatial scales, their interactions occur over different scales. For example, within a particular functional group, species that operate at larger scales require resources to be more aggregated in space than do species that operate at smaller scales.

Ecological resilience, as previously defined in Chapter 1, is a measure of the amount of change or disruption that is required to change a system from being organized around one set of mutually reinforcing processes and structures to operating around a different set (Holling 1973). This implies that ecosystems can have alternative self-organized states. In the cross-scale perspective proposed by Peterson et al. (1998), ecological resilience derives from overlapping functions within scales and the reinforcement of functions across scales. Cross-scale resilience complements within-scale resilience, which occurs when ecological functions overlap among the species of different functional groups that are operating at the same scales. Within a multi-taxa functional group, members that use similar resources may exploit different ecological scales. This leads to another form of ecological resilience as function is reinforced across scales (Peterson et al. 1998).

Perhaps the greatest challenge in the debate on biodiversity and ecosystem function is to reconcile community and ecosystem ecology in a framework that more explicitly includes humans. Traditionally, community ecologists have focused on explaining species diversity as a function of abiotic factors and interspecies interactions. On the other hand ecosystem ecology has focused on the role of biotic interactions in governing ecosystem processes and function. Humans influence both the biotic and abiotics forces that govern ecosystems. Understanding the mutual interactions and feedback among biodiversity changes, ecosystem functioning, and abiotic factors is a major challenge to achieving a true synthesis of community and ecosystem ecology. This is an essential step in better understanding the role of humans and articulating hypotheses about the interaction between human and ecological functions and biodiversity.

8.2 Urban Patch Dynamics

Over the last three decades, patch dynamics has emerged and evolved as a framework for studying the ways that pattern and process become coupled at different scales. It provides a promising approach to bridge theoretical and methodological gaps and to more effectively integrate community and ecosystem ecology. Patch dynamics explicitly recognizes that ecological systems are hierarchical, non-equilibrial, and vary both in time and space (Pickett and White 1985). The concept is essential to understanding the nature and dynamics of urban landscape ecology and the mechanisms of patch creation and evolution in urbanizing regions. While ecologists have recognized that heterogeneity results from environmental gradients (elevation, climate, etc.) at coarser scales, it is only in the last few decades that researchers in ecology have started to fully appreciate the implications of patch-level spatial homogeneity (Pickett and Rogers 1997).

Urban ecosystems differ from non-urban ones in their structure, processes, and functions (McDonnell and Pickett 1990, Rebele 1994, Trepl 1995). Based on the physical changes observed on the urban-to-rural gradient (Pickett et al. 1997), McKinney (2002) describes a biodiversity gradient in which species richness declines from the urban fringe towards the urban core. In the transition, as more and more habitat is lost, it is replaced by remnant, ruderal, and managed vegetation and built habitat, which vary in how habitable they are for most native species. As I suggested earlier, the key characteristic of urban ecosystems is their hybrid nature. To explain patterns of species diversity in urbanizing regions, we must look at the complex interactions between human processes and ecosystem processes that generate unique spatial and temporal heterogeneity. In turn, emerging patterns and processes of urban landscapes affect both biodiversity and ecosystem function.

What properties distinguish urban landscape patterns and processes from those of pristine ones? Trepl (1995) identifies three key sets of hypotheses related to integration, succession, and invasion. First, he says, in urban ecosystems the urban habitat patches and communities are not highly integrated, i.e. not well organized or connected; the systems are not in equilibrium, and stochastic processes predominate over deterministic ones (Trepl 1994). Second, succession in urban landscapes is hard to predict as the history and legacy of disturbances govern its dynamics. Third, urban ecosystems are open to invasions by unknown numbers of alien species.

Trepl (1995) observes that habitat patches and their species communities are less integrated in cities since patches are often isolated from each other by a matrix of built environment. These new barriers make dispersal difficult and potentially penalize organisms that are less able to move (Gilbert 1989, Rebele 1994). The impact of roads on wildlife dispersal in human-dominated environments has been extensively investigated (Forman 2000, Forman and Alexander 1998), and several strategies have been proposed to limit the negative effects of roads, but the multiple barriers created by urban development are still not fully understood. Offering a specific example, Davis (1978) noted that the best predictor of species richness of ground arthropods in London gardens was the proportion of green areas within a 1 km radius of the sampling site. Building on island biogeography and metapopulation dynamics, Klausnitzer (1993) and Weigmann (1982) have examined the relationship between species richness and patch area and found a consistent positive relationship. For birds, the built environment between green patches is not necessarily a barrier to dispersal, but fragmentation and change of habitat do affect their survival and success. Both dispersal and habitat requirements are modified in urban environments, favoring species that have both the ability to disperse and greater flexibility in habitat requirements (Gilbert 1989).

Human-induced disturbances in urban environments maintain urban habitats at an early successional stage (Trepl 1995, McDonnell et al. 1997, Niemala 1999a, 1999b). Some disturbances, such as fire and flooding, are suppressed in urban areas. At the same time, human-induced disturbances are more prevalent and persistent. Often, one part of the environment will be at an early successional stage (e.g., mown lawn) while another part is at climax stage (e.g., old trees). Furthermore, the patchy distribution of urban habitats, combined with the varying degree of human-induced disturbance and chance, results in a number of succession paths across habitat patches (Niemala 1999a). Even adjacent patches may exhibit very different successional paths depending on the colonization history of plants, which is largely determined by chance events (Gilbert 1989). This historical uniqueness and the overwhelmingly external control of succession are important features that distinguish urban habitats from more natural ones (Trepl 1995).

Urban ecosystems are simultaneously influenced by the environmental changes driven by humans and the ability of plants, animals, and microorganisms to adapt to and exploit these changes. Environmental conditions that differ between urban and rural areas favor certain species over others. Temperature is a good example: Many species requiring high temperatures thrive in cities where the temperatures are higher than in surrounding areas (Gilbert 1989). Bradshaw (2003) describes the phases of succession in urban areas by identifying the key ecosystem attributes and processes involved (Table 8.1). Urban structures provide unique opportunities for organisms—from abundant food sources to shelter (Bradshaw 2003).

Urban development creates new opportunities and challenges for species competition and predation, both as exotic species are introduced and as invasive species migrate in. Invasive or non-native species take advantage of poorly integrated communities and patches in the urban setting. This can be seen as a colonization process, as more frequent introductions of exotic species translate into invasions (Rebele 1994). Examples of this phenomenon abound. The proportion of alien plant species in Berlin increased from 28% in the outer suburbs to 50% in the built-up center of

Table 8.1. Succession in urban ecosystems (Bradshaw, 2003, p. 81).

Ecosystem Attribute	**Processes Involved**
Colonization by species	Immigration of plants species
	Establishment of those plant species adapted to local condition
Growth and accumulation of resources	Surface stabilization and accumulation of fine mineral materials
	Accumulation of nutrients particularly nitrogen
Development of the physical environment	Accumulation of organic matter
	Immigration of soil flora and fauna causing changes in soil structure and function
Development of recycling process	Development of soil microflora and fauna
	Possible difficulties in urban areas
Occurrence of replacement process	Negative interaction between species by competition
	Positive interaction by facilitation
Full development of the ecosystem	Further growth
	New immigration, including aliens
Arrested succession	Effect of external factors
	Reduction of development
Final diversification	The city as a mosaic of environments
	High biodiversity as a result

the city (Sukopp et al. 1979). Along a 140-km urban-to-rural environmental gradient originating in New York City, McDonnell et al. (1997) found lower levels of both earthworm biomass and abundance in the urban forests, compared to the rural forests. They attribute the difference to the incidence of introduced species. Insects are also successful invaders because of their ability to survive well around humans (Spence and Spence 1988). For instance, in western Canada, the 20 ground beetle (Carabidae) species of European origin account for the majority of carabids in cities (Niemela and Spence 1991).

8.3 Urban Ecosystem Processes and Biodiversity

Urban development affects biodiversity both directly, by altering the land cover and introducing non-native species, and indirectly, by changing ecosystem and biogeochemical processes. Urban impacts on biodiversity occur both locally and globally. At the global scale, the leading drivers of biodiversity loss are changes in landscapes and climate, and the introduction of non-native species. Humans' location choices are a major factor, since people prefer to settle on the most productive soil and in highly diverse areas. Recent findings have indicated that areas with the highest human population density and high biodiversity levels coincide when observed at the regional scale (Luck 2007, Pautasso 2007). This is true for plants, amphibians, reptiles, birds, and mammals across most regions of the world (Balmford et al. 2001, Araújo 2003, Luck et al. 2004, Evans and Gaston 2005, Real et al. 2003). But while this pattern is generally observed at the regional scale, the reverse is true at the local scale where people compete for resources with other species, making for a negative correlation between human presence and biodiversity (Beissinger and Osborne 1982, Clergeau et al. 2001, Fudali 2001, Moore and Palmer 2005). The correlation between human presence and species richness apparently depends on scale (Manne 2003, Váquez and Gaston 2006) which, according to Pautasso (2007), may provide a plausible explanation for findings that species richness peaks at intermediate levels of urbanization.

Although many researchers have tried to estimate the current loss and potential threats to biodiversity globally, we do not know how much species extinction or endangerment can be attributed to urbanization. Ewing et al. (2005) estimate that, of rarest and most imperiled species in the United States, 60% are threatened by rapid growth within the 35 fastest-growing metropolitan areas that are home to 29% of these species. They suggest that sprawl may lead to a great potential loss of species; whether or not these predictions turn out to be true, we know that many effects of sprawl threaten species survival. Though studies of human density and biodiversity have conflicting findings, the predominant pattern is a negative correlation between increasing human population density and species richness at a local scale. But the interactions are complex, and it is imperative that we better understand the mechanisms that govern biodiversity in urbanizing regions if we intend to reduce the impacts of urbanization.

Ecological studies have focused primarily on patterns of species diversity, aiming to establish relationships between the emerging urban landscape structure and the distribution, movement, and persistence of species on an urban-to-rural gradient (McDonnell et al. 1997). However, more recent studies have attempted to articulate the mechanisms governing biodiversity in urbanizing regions (Hansen et al. 2005, Faeth et al. 2005). By focusing on behavioral ecology, biotic interactions, genetics, and evolution, a few studies have revealed that urbanizing environments are a unique setting, in which human actions mediate fundamental patterns and processes in complex ways (Shochat et al. 2006). Despite this complexity, scholars of urban ecology agree that the challenge in the next decades is to formalize a theory of the mechanisms governing biological diversity where humans are present, and to resolve some long-standing unexplained contradictions between observations and ecological theories.

Findings from current urban ecological studies at the two Urban Long Term Ecological Research (LTER) sites in Baltimore and Phoenix, as well as in Seattle, provide important evidence that allows scholars to develop hypotheses on the mechanisms that drive urban biodiversity. Hypotheses about how humans impact species diversity can be articulated around key mechanisms that influence biodiversity: habitat productivity, species interactions, trophic dynamics, heterogeneity, disturbance, and evolution.

Habitat productivity

Productivity— "the rate at which energy flows through an ecosystem" (Rosenzweig and Abramsky 1993)—is one of the ecosystem properties in urbanizing regions that may explain patterns of species diversity along the urban-to-rural gradient. But the mechanisms that govern the relationship between productivity and species richness are far from being understood (Waide et al. 1999). Although most scholars agree that productivity affects species richness at large scales (Waide et al. 1999), studies show contradictory results. Two types of relationship between productivity and diversity have been proposed: (1) monotonic, where diversity increases as productivity increases at the regional and global scales; and (2) unimodal, where diversity increases along with increasing productivity but declines at the highest productivity levels, primarily at the local scale (Abrams 1995).

This latter hump-shaped relationship has been proposed to describe the ways productivity, urban population density, and species diversity are related to each other (Blair 1996, Marzluff 2001). Since highly developed areas have a net primary production (NPP) close to zero, we should expect to find lower species richness in them. In Seattle, for example, densely populated urban areas are associated with lower bird diversity (Marzluff 2001). NPP mediates the relationship between anthropogenic land cover change and both faunal and plant species richness (Mittelbach et al. 2001), although the relationship is dependent on scale (Waide et al. 1999). At the urban fringe, in highly managed landscapes, high species richness is often associated with a higher local rate of productivity relative to the surrounding areas. Shochat et al. (2006) suggest that habitat productivity in managed urban green spaces is generally higher compared with the surrounding areas because of the high human resource input. Although they recognize that the high productivity levels are limited to the urban fringe where green patches represent a larger proportion of the landscape. In fact, Imhoff et al. (2000) found evidence of this relationship by analyzing the NPP for the 48 contiguous states. They found total NPP to be higher in urban areas than in wildlands, both in cities located in arid environments and in low-density development (Imhoff et al. 2000, 2004).

Although the relationship between habitat productivity and diversity is generally unimodal, the strength, shape, and sign of the relationship vary with scale of observation (Mittelbach et al. 2001). In urban regions, we can expect that the productivity-diversity relationship will vary both with biophysical characteristics as well as with urban form (Shochat 2006). Complex interactions and especially feedback between diversity and productivity (Naeem et al. 1996, Tilman et al. 1996) have not been studies in urban setting. And since different mechanisms operate at multiple scales, studies of urban ecology must incorporate a hierarchical approach (Cleargeau et al. 2006). These investigations are essential to better understand the role that humans play in mediating this relationship.

Biotic interactions

Urbanization affects ecosystem function by altering the way species are distributed and interact with each other (Marzluff 2001, Hansen et al. 2005). For example, both native and nonnative predators may increase near human settlements, a change that may then affect other native species. Species found at the urban fringe are edge-adapted generalists who are able to use most effectively a variety of natural and human-generated resources for their survival (McKinney 2002). Higher densities of nest predators explain high rates of nest predation of migratory songbirds in suburban woodlots in

Maryland (Wilcove 1985). Another mechanism that lowers diversity is competition. Species often colonize urban areas within regions where they would not normally thrive. Examples include the grey-headed flying foxes (*Pteropus poliocephalus*) in Melbourne, Australia (Parris and Hazell 2005) and the house gecko (*Hemidactylus frenatus*) in Hawaii (Petren and Case 1996). As such species become more abundant, the native urban species, usually good adapters, could become extinct locally (Shochat et al. 2006).

How different are the key processes governing the diversity of an urbanizing ecosystem from the compensatory processes of colonization and extinction that are postulated by island biogeography theory (MacArthur and Wilson 1963, 1967)? For cities, the high turnover of species is primarily affected by the introduction, dispersal, and local extermination mediated by human activity (Rebele 1994). Marzluff (2005) developed a graphical model to form a series of testable hypotheses about how extinction and colonization are affected by urbanization in determining local diversity. Colonization and extinction, the fundamental processes governing diversity, respond to organisms' rates of survival, reproduction, and dispersal (Marzluff and Dial 1991, Bolger 2001). In human dominated ecosystems, colonization and extinction are affected by changes in land cover, the removal of barriers to dispersal, the introduction of new species, and the action of new selective forces caused by changes in climatic regimes, predators, competitors, and diseases (Marzluff 2005, Husté and Boulinier 2007). And while diversity still emerges as the balance between extinction and colonization, species invasion plays a prominent role (Olden and Poff 2003, 2004, Marzluff 2005).

Trophic dynamics

Human activities in cities alter the food webs and trophic structure of biological communities. Ecologists have studied the factors that control the trophic structure and function of ecosystems for quite some time, but they have not thoroughly studied the trophic organization of urban areas (Faeth et al. 2005). Faeth et al. (2005) point out the importance for ecology to understand the structure and function of food webs in urban settings not only because urban habitats are increasingly important, but also because this knowledge is crucial to conservation efforts. Conservation planners and managers need to know what controls the number and diversity of trophic levels in urbanizing regions and how species in food webs interact through the processes of competition, predation, parasitism, and mutualism.

Urban habitats affect both above- and belowground food-webs (Bramen et al. 2002). Studies of the Sonoran Desert, developed as part of the Central Arizona-Phoenix LTER (CAP LTER), reveal some surprising human-induced modifications with respect to factors controlling trophic dynamics, according to Faeth et al. (2005). They found that species composition was radically altered (e.g., generalist species increased), and that resource subsidies caused by people increased and stabilized productivity (i.e., via modified water availability). This supports their hypothesis that the absence or reduction of predators and the increased abundance and predictability of resources in urban areas may cause a shift in control from top-down to bottom-up. Based on the Phoenix study, they propose that urbanization caused shifts from a system that is resource-based or controlled from the bottom up—typical of the Sonoran Desert—to a combined bottom-up and top-down model.

Spatial and temporal heterogeneity

The diversity of species in urbanizing regions is greatly affected by the quality of habitat and template of resources. These factors are the results of biophysical processes operating at multiple scales and mediated by human actions. Ecosystem processes are heterogeneous and highly related to species distributions (Turner and Chapin 2005). The *habitat heterogeneity* hypothesis states that greater spatial variation in physical or environmental conditions allows for greater niche differentiation and, hence, more species (MacArthur and MacArthur, 1961). Humans affect habitat quality and resource availability by changing habitat heterogeneity in space and time. In urbanizing regions both spatial and temporal heterogeneity are influenced by human and biophysical processes associated with high fragmentation of land use and management.

The effect of human action on spatial heterogeneity in urbanizing regions is very well documented; however, how we know less about how this heterogeneity varies with scale, partly because studies have tended to focus primarily on aggregated measures (Band et al. 2005). At the scale of meters or below, urbanization may reduce the heterogeneity of land cover, but at the patch level, it may introduce highly heterogeneous new biophysical conditions as the varied behaviors of land owners result in fragmented management patterns. As the scale increases, we may observe a further reduction in heterogeneity due to consistent patterns of urban development and habitat fragmentation.

Changes in temporal variability in urban ecosystems are driven by both human structures and high inputs of resources. A good example of change in temporal heterogeneity is the buffering effect that microclimatic changes associated with urbanization can have on habitat: In temperate cities, heat islands can extend the growing season while in desert cities, they can cause thermal stress and extend droughts. Shochat et al. (2006) report that the heat island in Phoenix, Arizona, has increased the stress on cotton plants (*Gossypium hirsutum*). Highly managed green areas in temperate cities such as Seattle, and irrigation in semi-arid cities such as Salt Lake City, provide water for plants throughout the year with subtle effects on wildlife.

Urban management and the built infrastructure can artificially reduce the variation—in both space and time—of resource availability, thus altering seasonal variations and dampening temporal variability. Some species thrive when they have less variation to endure, and their urban populations rise. A well-known example is the grey-headed flying-fox (*Pteropus poliocephalus*), a large, nomadic bat from eastern Australia that became established in Melbourne, Australia, when a heat island effect led to long-term climatic changes. Parris and Hazell (2005) found that human activities have increased temperatures and effective precipitation in central Melbourne, creating a more suitable climate for camps of the grey-headed flying-fox. Changed habitat, due to the high availability of water and continuous availability of food, interacts with biotic, trophic, and genetic processes and may help some species adapt to urban environments.

Heterogeneity in urban ecosystems is driven simultaneously by natural and human agents and processes. Urbanization tends to increase spatial and temporal heterogeneity on some scales and reduce it on others. For example, urban development enhances spatial variability by fragmenting the land cover. At the same time, the built landscape and infrastructure tend to decrease heterogeneity within patches and at larger scales. As a result, carbon, water, nutrient, and energy cycling are highly modified (Band et al. 2005). Increases in heterogeneity can also favor certain species and penalize others, changing biotic interactions and community composition. Furthermore, spatial heterogeneity affects disturbance regimes, and is another fundamental mechanism that links urban patch dynamics to ecosystem process and function.

Disturbance regimes

Ecosystem disturbances are events that affect the pathways by which matter or energy flows in an ecosystem (Pickett et al. 1999). Disturbances affect resource availability (i.e., water and nutrient), ecosystem productivity, and species diversity. Changes in resources and related ecosystem processes caused by anthropogenic disturbances affect plants and animals over time, and ultimately successional dynamics. Urbanization modifies existing disturbance regimes (e.g., through fire and flood management) and creates novel disturbances (e.g., through new or disrupted dispersal pathways or species introduction). Cardinale et al. (2006) suggest that disturbance can moderate relationships between biodiversity and ecosystem functioning in two ways. It can increase the chance that diversity will generate unique system properties (i.e., emergent properties), or it can suppress the probability of ecological processes being controlled by a single taxon (i.e., the selection-probability effect).

As urbanization changes disturbance regimes, it affect species diversity (Rebele 1994). Species diversity is high at intermediate frequency or intensity of disturbance (Connell 1978, Pickett and White 1985). Disturbance impacts directly species interaction by precluding competitive dominance (Poff et al. 1997) and Cardinale et al. (2000) articulates the mechanisms by which disturbance mediate the relationship between species diversity and ecosystem function by focusing on variation of species abundance across scale. More recently Cardinale and Palmer (2002) use a laboratory experiment to show that indeed disturbance mediates the response of stream ecosystems to species richness.

Evolutionary processes

Humans influence evolutionary processes by changing speciation and extinction patterns (Palumbi 2001). For example, humans are challenging bacteria with antibiotics, poisoning insects, rearranging and exchanging genes, creating and dispersing thousands of synthetic compounds, and fishing selectively. By hunting, moving around the globe, and massively reconfiguring the planet's surface, humans have increased species extinction rates to levels 1,000 to 10,000 times higher than those resulting from nonhuman causes, through resulting changes in predation and competition (Pimm et al. 1994, Vitousek et al. 1997, Flannery 2001). The combined effect of changing speciation and extinction is rapid evolutionary change (Palumbi 2001).

Urban environments may facilitate speciation by bringing together species previously isolated, or isolating populations through habitat destruction, as well as by introducing new exotic species, phenomena of speciation are much more likely to occur (Sax and Gaines 2003). Chances of extinction, on the other hand, are increased by changes in habitat and selective forces (Ledig 1992). In urban environments, selective changes are caused by eliminating variation in resource availability (i.e., food and water) and modifying biotic interactions (i.e., predation). Humans in cities also create new selective forces affecting the genetic structure and diversity of urban ecosystems (Yeh and Price 2004).

The evolution of behavioral flexibility and adaptive phenotypic plasticity in response to spatial and temporal variation in species interactions in urban environments can facilitate the success of organisms in novel habitats, and potentially contributes to genetic differentiation and speciation (Agrawal

2001). Adaptation generally does not occur in a relatively short period of ecological time. But in urban environments, resource availability and lower risks of predation may facilitate persistence until genetic change occurs. Wood and Yezerinac (2006) hypothesize that song sparrows have changed the frequency of their notes to adapt to the noisy urban environment. Another example is the dark-eyed junco (*Junco hyemalis*) reveals how this species has adapted its tail feathers in San Diego, California (Yeh and Price 2004). At the same time, the extreme turnover in biological communities might prevent the genetic differentiation of urban populations and impede evolutionary responses to the novel selective forces associated with urbanization (Shochat 2006).

8.4 The Intermediate Hypothesis: A Case Study in the Puget Sound

The intermediate disturbance hypothesis is a nonequilibrium ecological hypothesis that provides an explanation for the coexistence of species in ecological communities based on complex coexistence mechanisms (Wilson 1994, Dial and Roughgarden 1998, Buckling et al. 2000). It also suggests that in a situation of intermediate disturbance, more species can be expected at a given instant in time, whether or not that diversity is maintained over the long term (Roxburgh et al. 2004).

To test this hypothesis in urbanizing regions, researchers have studied many taxa including mammals (Racey and Euler 1982), birds and butterflies (Blair and Launer 1997, Blair 2001), ants (Nuhn and Wright 1979), and plants (Kowarik 1995). Birds are excellent indicators of the effects that urbanization has on ecosystems since they are highly mobile and respond rapidly to changes in landscape configuration, composition, and function (Marzluff et al. 1998). Urbanization affects birds directly as the ecosystem processes change, along with habitat and food supply. In fact, the percentage of land cover that is vegetation is a good predictor of the number of bird species. Birds are also affected indirectly as urbanization influences other factors, especially predation, interspecies competition, and diseases (Marzluff et al. 1998). Urbanization increases the number of introduced species and drastically reduces the number of native species (Marzluff 2001), thus altering the composition of urban avian communities. Populations of native species decline because their natural habitats are reduced and they cannot tolerate human disturbances (Beissinger and Osborne 1982, Blair and Walsberg 1996).

As part of a Biocomplexity project, we examined the interactions and feedback between urban development and land cover change and the effects on bird diversity in the Central Puget Sound region (Alberti et al. 2006a). Led by Marzluff, a team of wildlife biologists are studying the response of birds to the complex landscape changes produced by urbanization. Marzluff (2005) found that songbird diversity peaks in landscapes with 50% to 60% forest cover, because such areas gain more synanthropic birds (those that benefit from contact with humans) and more successional species; Meanwhile, some of the native forest species tend to leave such areas. The birds' dynamic response to changing land cover allows us to demonstrate how one component of biological diversity might respond to urbanization.

Study area and avian surveys

The bird study area is the Puget Sound lowland (<500 m above sea level) (3,200 km^2) of temperate, moist forest surrounding Seattle, Washington. 139 study sites of 1 km^2 were selected and characterized according to their land use. Of the 139 sites, 119 were characterized as single-family residential (SFR), 13 as mixed use/commercial/industrial, and seven as forested ("control") sites with minimal development (Marzluff et al. 2001). The team also randomly selected 126 single-family residential and forested control sites along several axes of urbanization including: 1) urbanization intensity, 2) mean patch size of urban land cover, 3) similarity of adjacent areas, and 4) development age. The sites defined as suburban contained >70% urban land cover, and <15% forest land cover. The exurban sites contained <50% urban land cover, and >40% forest land cover (Alberti et al. 2004). During the springs and summers of 1998 through 2005, trained observers conducted 6437 fixed-radius (50 m) point-count surveys of breeding birds at 992 locations within the 139 study landscapes. (For a full description of the study see Donnelly and Marzluff 2004a, 2004b, 2006, Blewett and Marzluff 2005, and Hepinstall et al. in press).

Observations

Marzluff (2005) shows that birds respond to human settlement along an urban-to-rural gradient in a complex way. The number of bird species in a 1 km^2 landscape made up of single-family housing and fragments of native coniferous forest was strongly correlated with the percentage of forest. The relationship is non linear (Richness = 17.7 + 46.03 (% forest) – 42.9 (% forest)^2; $F_{2,56} = 22.3$, $P < 0.0001$) as shown in Figure 8.2. The quadratic relationship accounted for nearly half of the variation in bird species richness ($R^2_{adjusted} = 43.2\%$) (Marzluff 2005).

The richness peaked at the ratio of approximately 50% forest in the landscape. The richness of bird species is determined by the balance between two factors: the retention of native forest birds and the addition of synanthropic and early successional species. Species gain was quadratically related to the amount of forest. The number of native bird species that remained decreased only slightly as the amount of forest increased. Thus, bird communities in landscapes of 50% 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 human activities. Bird communities in more urban areas are impoverished because only about ten synanthropic species live on the mostly paved landscapes, along with fewer than five native species. Likewise, communities in the mostly forested areas are impoverished because they are composed almost entirely of the fifteen native forest birds.

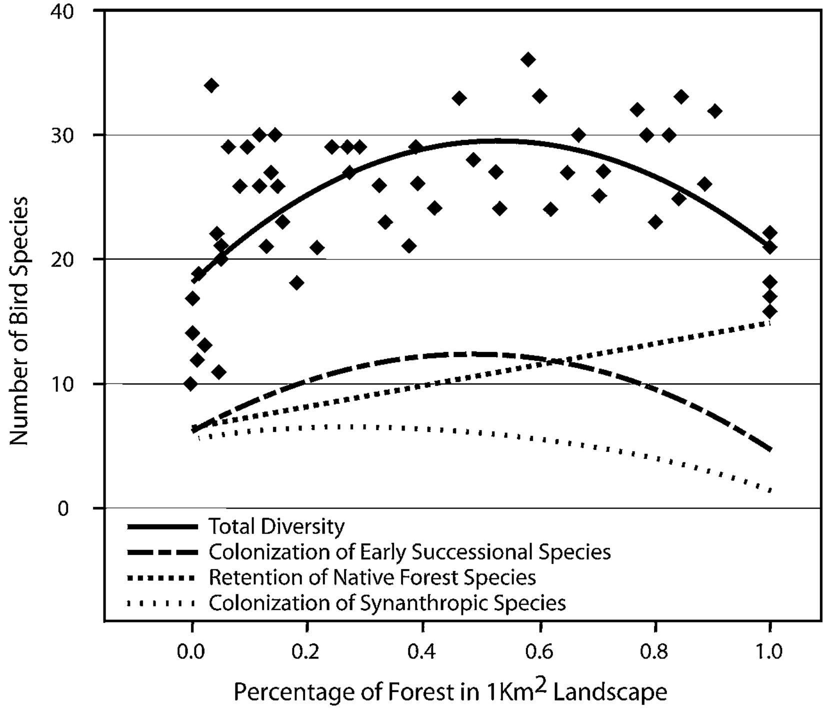

Figure 8.2. Impact of urbanization on songbirds. Measures of total species richness, which peaked at approximately 50% forest cover, reflect the combined effect of a steady decline in native species with decreasing percentage of forest cover and an increase in early successional and synanthropic species, which benefit from human activities with decreasing forest. The lower species richness at very low levels of forest cover (i.e., more heavily paved urban areas) reflects the dominance of a smaller number of more competitive synanthropic and remnant native species. Similarly, lower richness measures at higher levels of forest cover reflect the presence of predominantly native bird species (Marzluff 2005, p. 166).

Statistical models

To predict future patterns of richness and relative abundance of bird species, we developed a coupled model of land cover change and bird diversity by linking the land cover change model (LCCM) and a series of statistical models of birds' responses to change in landscape composition and configuration (Hepinstall et al. in press). Marzluff et al. (2001) used point-count data from the 139 study landscapes to develop separate models of species richness for all the species and the three development-sensitive guilds (Marzluff et al. 2001). The study involved a land cover characterization of each 1 km^2 bird study area based on land cover data from 2002 to calculate the percent forest, percent urban, and aggregation index (Fragstats 3.3, McGarigal et al. 2002) of the forest, as well as the number of patches of forest, and the number and mean size of the urban patches. To better characterize the study sites, Hepinstall et al. (in press) used land use information derived from 2002 parcel data to calculate the percent patch density, and aggregation index of residential parcels, and the development age of all the parcels within each study area.

Marzluff and Hepinstall developed two *a priori* models of species richness and relative abundance based on previous studies (e.g., Donnelly and Marzluff 2004a, 2004b, 2006, Hepinstall et al., in press), on landscape measures relevant to urban planners, and on variables available as output from our LCCM. A first simple model (SM) included: 1) percentage of forest (in linear and quadratic form); 2) aggregation of residential land use; and 3) development age of parcels within a 1-km^2 window. A more complex model (FM) added seven more variables: 1) percentage of grass and agriculture; 2) forest aggregation index; 3) number of unique patches of forest land cover; 4) number of unique patches of urban land cover; 5) mean patch size of unique patches of urban land cover; 6) percent of residential land use; and 7) patch density of residential land use.

Applying the parameter estimates from models of species richness and relative abundance to the future landscapes generated by the land cover change model, Hepinstall et al. (in press) predicted the total guild- and subguild-specific species richness, and relative abundance for all species.

Future land cover and avian diversity

Our LCCM predicts that in the next two decades we will observe a decline in mature forest types (deciduous, mixed, and coniferous) from 60% of the study area to 38%, and an increase in developed land (heavy, medium, and low urban classes) from 17% to 34%. According to our model, the proportion of land in grass and agriculture will decrease from 14% to 10% of the area, while the proportion of clearcut and regenerating forest will increase from 9% in 2003 to 18% in 2027 (Alberti et al. 2006a, Hepinstall et al. in press). This substantial reduction in forest cover and increase in developed land will affect the region's avian populations. Although, overall, only three to five species are expected to be lost, the loss in ecological resilience due to forest loss and fragmentation will make bird diversity significantly more vulnerable to future loss of forest. In addition, the observed pattern of avian diversity along the gradient of urbanization has an influence on the overall avian population dynamic.

The spatially explicit land cover change predictions can be mapped to explore the local effects of landscape change. We expect that changes in species richness will be concentrated in those regions of the study area where land cover change is most dramatic, primarily in the transition development zone surrounding the present heavy urban core where forest loss and aging of developments are more pronounced. We see similar patterns of loss in richness for the total species, the native forest species, and the early successional species. We predict a species loss at any specific locale up to 23 species, and up to nine species lost respectively from the native forest and early successional guilds. The model predicts a gain for the synanthropic species of two to four species in the transition zone.

Changes in the landscape pattern in the central Puget Sound region will affect the diversity of the transition zone. Currently, avian diversity peaks at the transition zone and exurban zones, but we expect that in the near future as the transition zone shifts, avian communities will gradually become more diverse the farther they are from development, rather than peaking at an intermediate level of settlement. (Figure 8.3).

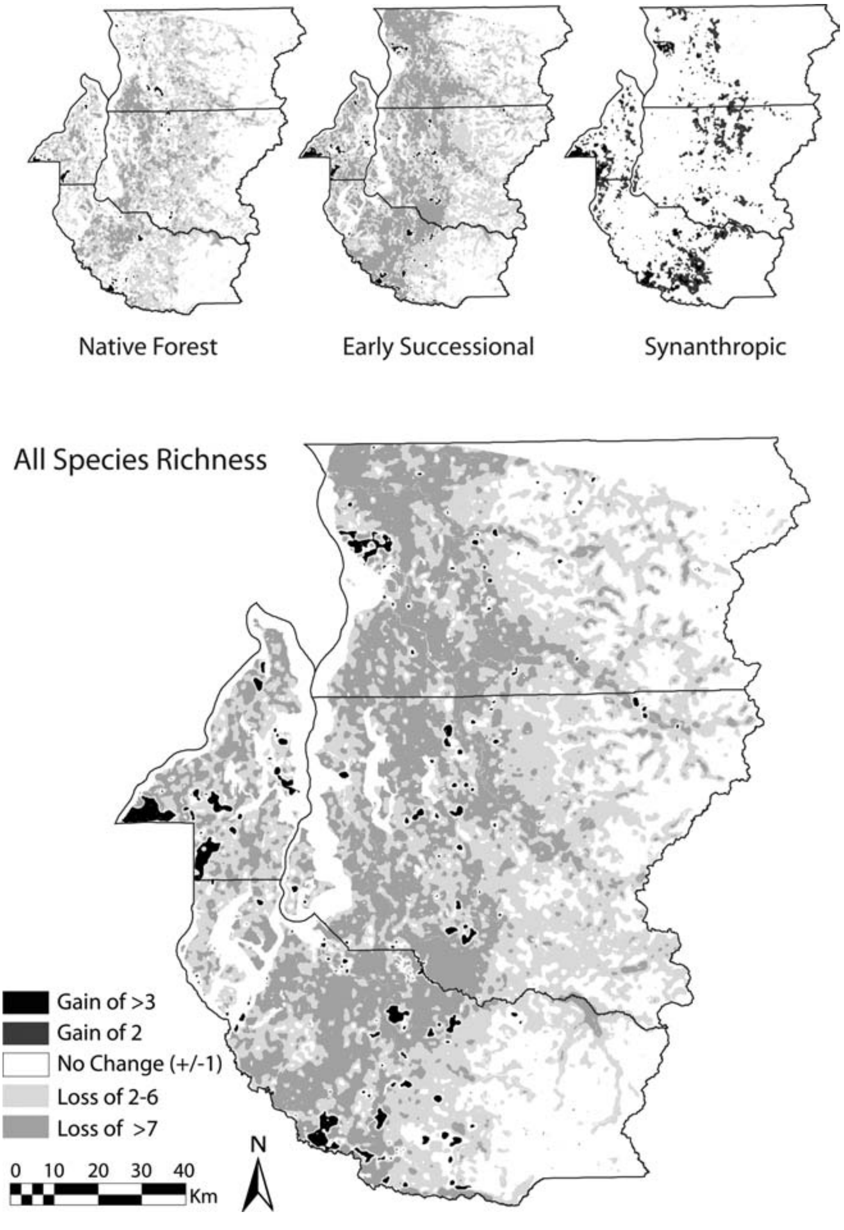
Native Forest
Early Successional
Synanthropic
All Species Richness
Gain of >3
Gain of 2
No Change (+/-1)
Loss of 2-6
Loss of >7
0 10 20 30 40
Km
N

Figure 8.3. Change in bird diversity in Central Puget Sound. The maps illustrate locational changes in abundance of native forest, early successional, synanthropic, and total bird species in the central Puget Sound region. Areas exhibiting significant losses in species richness reflect highly urbanized regions (e.g., the greater Seattle metropolitan area, center) mostly dominated by small numbers of synanthropic species, whereas gains in (mostly synanthropic) species along the Cascade range to the east of Seattle reflect areas exhibiting significant conversion of forest to other land uses (e.g., development, forest harvesting, etc.) (Hepinstall et al. in press).