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THE EFFECTS OF URBAN PATTERNS ON ECOSYSTEM FUNCTION

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Urban ecological systems are characterized by complex interactions among social, economic, institutional, and environmental variables. These interactions generate complex human-dominated landscapes, which significantly influence the functioning of local and global earth ecosystems and the services they provide to humans and other life on earth. Urban development fragments, isolates, and degrades natural habitats; simplifies and homogenizes species composition; disrupts hydrological systems; and modifies energy flow and nutrient cycling. Urban areas also appropriate a large share of earth's carrying capacity from other regions in terms of resource input and waste sinks. Change in ecological conditions that result from human actions in urban areas ultimately affect human health and well-being. In this article, the author reviews the empirical evidence on the effects that patterns of urban development have on ecosystem function. Urban development affects the spatial heterogeneity of the landscape (i.e., pattern of variation in land cover) and spread of disturbance (i.e., invasive species). The author proposes that alternative urban patterns generate differential ecological effects. The review reveals that the interactions between urban development patterns and ecosystem dynamics are still poorly understood. The author draws on an empirical study of the Puget Sound metropolitan region currently developed at the University of Washington to propose directions for future empirical research that can inform strategies to minimize urban impacts on ecosystems.

Keywords: *urban ecology; landscape ecology; land-use patterns; biodiversity; ecosytem function*

1. INTRODUCTION

The future of earth ecosystems is increasingly dependent on the patterns of urban growth. Cities are growing rapidly worldwide. The world's urban population[1] has multiplied more than tenfold during the past century, from 224 million in 1900 to 2.9 billion in 1999 (United Nations [UN] 1999). It has also risen from 14 to 50 percent of total world population. In 1900, only sixteen cities had a population exceeding 1 million; by 2000, more than four hundred did. By the year 2030, more than 60 percent (4.9 billion) of the estimated world population (8.1 billion) will live in cities: 56.2 percent of the population of developing countries (3.88 billion) and 83.5 percent of that of the developed countries (1.01 billion) (UN 1999). The

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world's urban population will grow at an average annual rate of 1.8 per cent, nearly double the rate expected for the total population of the world (1 percent per year).

Urbanization significantly influences the functioning of local and global earth ecosystems and the services they provide to humans and other life on earth. Urban development fragments, isolates, and degrades natural habitats; simplifies and homogenizes species composition; disrupts hydrological systems; and modifies energy flow and nutrient cycling (Alberti et al. 2003). While urbanized area accounts only for ~ 1 to 6 percent of the earth surface, cities appropriate a large share of earth's carrying capacity in terms of resource input and waste sinks. Since humans depend on earth ecosystems for food, water, and other important products and services, changes in ecological conditions that result from human actions in urban areas ultimately affect human health and well-being.

Urban regions are increasingly capturing the attention of ecological scholars. They provide challenges and potential insights to the ecological discipline (Alberti et al. 2003). Highly concentrated human populations cause changes in natural disturbances (i.e., more frequent flooding) and unprecedented disturbances (i.e., chronic stresses). The intensity of such disturbances are expected to change predictably with distance from the intense urban core (McDonnell et al. 1997). How alternative urban development patterns influence ecological systems along this gradient, however, is not known. Although many studies have addressed the relationship between urbanization and ecosystems (McDonnell and Pickett 1993), few have asked directly how alternative urban patterns control the distribution of energy, materials, and organisms in urban ecosystems (Sukopp, Numata, and Huber 1995; Alberti et al. n.d.). Most studies of the impacts of urbanization on environmental systems correlate changes in environmental systems with simple aggregated measures of urbanization (e.g., human population density, percentage impervious surface). We do not know, for example, how clustered versus dispersed and monocentric versus polycentric structures differently affect environmental conditions. Nor do we understand the ecological trade-offs associated with different housing and infrastructure densities.

In this article, I review the empirical evidence on the effects that urban development has on ecosystem function (Alberti 1999b, 1999c). To systematically review the impacts of urban development patterns (i.e., clustered vs. dispersed) on ecosystem functions (i.e., nutrient cycling), I apply a framework developed by Alberti et al. (2003) for studying urban ecosystems (Figure 1). I propose that interactions between humans and biophysical processes in urban landscapes are mediated by *patterns* of urban development. The *mechanisms* by which urban development affects ecosystem functions include the change in land cover and modification of natural disturbance that have distinct *ecological effects*. In spite of increasing ecological research in urban areas, I conclude that the relationship between urban patterns and ecosystem dynamics are still poorly understood. I build on an empirical study of the Puget Sound metropolitan region currently developed at the University of Washington (Alberti et al. n.d.; Alberti and Marzluff 2004) to discuss directions for future research that can inform strategies that minimize urban impacts on ecosystems.

2. COMPLEX URBAN LANDSCAPES

Cities differ from other ecosystems in several ways (Trepl 1995; Sukopp, Numata, and Huber 1995; Niemala 1999). Ecological scholars have described the city as a heterotrophic ecosystem highly dependent on large inputs of energy and materials and a vast capacity to absorb emissions and waste (Odum 1963; Boyden et al. 1981; Collins et al. 2000). Compared to a "natural" ecosystem with a typical energy budget ranging between 1,000 and 10,000 Kcal per square meters per year, cities consume a vastly larger amount of energy. The budget of an urban ecosystem in an industrialized country can range between 100,000 and 300,000 Kcal per square meter per year (Odum 1997). Other key differences in urban ecosystems are the lack of integration of habitat patches, the invasion of nonnative species, and the external control of succession (Trepl 1995). Furthermore, urban ecosystems differ from natural ecosystems also in microclimate (they are warmer and have greater precipitation), hydrology (increased runoff), and soils (higher concentrations of heavy metals and organic matter and abundant earthworms).

Urban landscapes are also different in their patch dynamics (Wu and Loucks 1995; Pickett and Rodgers 1997). Ecological scholars have started to investigate how spatial heterogeneity in urban regions influences the flow of energy, materials, species, and information across the urban landscape. Machlis, Force, and Burch (1997) described the urban landscape as a complex mosaic of biological and physical patches within a matrix of infrastructure and social organization. Spatial heterogeneity within an urban ecosystem is generated by both biophysical and human processes (Pickett, Cadenasso, and Jones 2000). Disturbances in ecology are any relatively discrete event in space and time that disrupts ecosystem, community, or population structure (White and Pickett 1985). Natural disturbances are modified in cities and heterogeneity of natural habitat reduced by human activities (Pickett and Rogers 1997). Human sources of heterogeneity include the introduction of exotic species, modification of landforms and drainage networks, control or modification of natural disturbance agents, and the construction of extensive infrastructure (Pickett, Cadenasso, and Jones 2000).

Social and natural scientists increasingly recognize the need to investigate complex interactions between humans and ecological processes in urbanizing regions and the limitations of traditional approaches applied to investigate these interactions in previous studies of urbanization. Ecological research has tended to reduce the human dimension of ecological studies in urbanizing landscapes to a few aggregated variables such as population density or built-up density that are expected to change predictably with distance from the urban core. Furthermore, in most ecological studies, cities are described as monocentric agglomerations, whereas most U.S. metropolitan areas over the past few decades have changed from a monocentered to a polycentric structure (Gordon, Richardson, and Wong 1986; Cervero and Wu 1995). In addition, urban-to-rural gradients in these studies are often represented as simple geographical transects from the urban core to ex-urban rural areas in place of the complex patterns emerging by the spatial distributions of land use and land cover.

Social and economic studies, on the other hand, have tended to oversimplify the diverse environmental factors that drive or are affected by socioeconomic patterns. These studies rarely discriminate across diverse biophysical and ecological processes or among different species. As a result, strategies devised to minimize ecological impacts of urban growth often fail to identify key underlining mechanisms that link urban patterns to ecosystem functions (i.e., interactions between extent and distribution of impervious surface and pollution generation caused by roads to affect stream conditions) and to understand the trade-offs that exist among different ecological processes (i.e., trade-offs among species).

More recently, several disciplinary approaches have been combined to study the interactions between complex human behaviors and ecosystem function (Grimm et al. 2000; Pickett, Cadenasso, and Jones 2000; Alberti et al. 2003). Scientists have started to recognize that urban ecosystems consist of several interlinked subsystems—social, economic, institutional, and environmental—each representing a complex system of its own and affecting all the others at various structural and functional levels. In studying the interactions between humans and ecological processes in urban ecosystems, we need to consider that many socioeconomic and biophysical factors work simultaneously at various levels with important feedback mechanisms. These complex interactions give rise to emergent phenomena whose properties cannot be understood by studying the properties of the socioeconomic and ecological systems in isolation.

Scholars of both urban economics and ecology have begun to recognize the importance of explicitly representing the interactions between human and ecological processes in studying urban regions (Grimm et al. 2000; Alberti 1999; Alberti et al. 2003; Pickett et al. 2001). Humans are the dominant driving force in urbanizing regions, and changes in environmental conditions also control human decisions. Furthermore, these interactions are spatially determined. The evolution of land uses and their ecological impacts are a function of the spatial *patterns* of human activities and natural habitats, which affect both *socioeconomic* and *ecological processes* at various scales. For example land-use decisions are highly influenced by patterns of land uses (e.g., housing densities), infrastructures (e.g., accessibility), and land cover (e.g., green areas). These local interactions affect the composition and dynamics of whole metropolitan regions.

2.1. URBAN PATTERNS

Several authors have hypothesized that alternative urban patterns have differential effects on ecosystems and their functions (Howard 1898; Lynch 1961, 1981;

Boyden et al. 1981; Douglas 1983; Owens 1984, 1986; Owens and Rickaby 1992; Breheny 1992; White and Whitney 1992; Jenks, Burton, and Williams 1996). But few have empirically examined how urban patterns affect energy and material flows either directly, by redistributing solar radiation and mineral nutrients, or indirectly, by determining the resources needed to support human activities. While many scholars have focused on the ecological structure and functions of habitat within cities (McPherson et al. 1997) or quantified their overall biogeochemical budget (Grimm et al. 2000), we do not know how they correlate with patterns of urban development.

Despite the increasing interest of ecology in studying urban areas, ecological scholars of urbanization typically simplify the consideration of urban structures to such an extent that the results of ecological studies are not useful to urban planners and managers. Few studies explicitly address how urban patterns affect ecosystem function (Grimm et al. 2000; Picket et al. 2001; Alberti et al. 2003). Most ecological studies in urban areas correlate conditions in environmental systems with aggregated measures of urbanization (e.g., built-up area, human population density: Wolman 1967; Leopold 1968; Berry 1990; McDonnell et al. 1997; Pickett and Cadenasso 1995).

From an ecological perspective, urban development affects patch structure by altering the size, shape, interconnectivity, and composition of natural patches. It also produces a variety of unprecedented and intense disturbances through physical changes in the landscape. Various configurations of the urban structure imply alternative outcomes in the mosaic of patches and, thus, differential effects on ecosystem function. Since urban development alters ecological conditions through physical changes, alternative urban patterns are expected to generate differential ecological effects (Forman and Godron 1981). Patch structure (size, composition, persistence, and interconnectivity) is important to species survival, and the ecological conditions of any patch are related to patch characteristics. Urban patterns also influence the feasibility of using alternative systems to supply resources and services such as public transportation, energy, and drinking water to the urban population, thus indirectly affecting their ecological impact (Alberti and Susskind 1997).

Landscape ecologists have started to document the impact that various arrangements of patch structure have on ecosystem functions (Godron and Forman 1982; Turner 1989; Forman 1995; Collinge 1996). In landscape ecology, the patch is the fundamental element of the landscape. The size and shape of the patch and its edge are particularly important patch characteristics that can affect species habitat, resource availability, and competition. Native plant and animal species in isolated patches decline with patch size as a result of habitat loss and interspecific interactions (Harris 1984; Soulé et al. 1988; Bolger, Alberts, and Soulé 1991; Dickman 1987). Native species are also affected by the edge effect (Ranney, Bruner, and Levenson 1981; Chen, Franklin, and Spies 1992) and reduced connectivity (Collinge 1996). Furthermore, the loss of habitat heterogeneity often associated with urbanization has negative effects on species richness (Newmark 1987). These characteristics of patch structure not only affect the chance of species survival. They also help maintain the integrity of various biophysical processes—prevent soil erosion, mitigate flooding, and protect water quality (Naiman and Decamps 1990).

Drawing on these empirical results, it is possible to articulate several testable hypotheses that link urban patterns and ecological conditions. Several dimensions of urbanization can directly be linked to patch structure and processes through urban form, land use intensity, land use heterogeneity, and land use connectivity (Alberti, Botsford, and Cohen 2001). Urban *form* refers to the degree of centralization of the urban structure. Land use *intensity* is the ratio of population or jobs to area. Land use *heterogeneity* indicates the diversity of functional land uses such as residential, commercial, industrial, and institutional. Land use *connectivity* measures the interrelation and mode of circulation of people and goods across the location of fixed activities. Each addresses some aspect of landscape structure, function, or change and can be useful in understanding ecosystem processes in urbanizing landscapes.

Researchers in landscape ecology have developed a large number of possible metrics for quantifying such patterns and their effects on ecosystems (O'Neill et al. 1988; Turner 1989; Gustafson and Parker 1992; Li and Reynolds 1993; McGarigal and Marks 1995; Gustafson 1998). In landscape ecology, these metrics are good predictors of the ecosystem's ability to support important ecosystem functions (Turner and Gardner 1991). These metrics can be applied to measure the *composition* and *spatial configuration* of urban landscapes (Alberti et al. 2001). Landscape composition metrics measure the presence and amount of different patch types within the landscape, without explicitly describing its spatial features (i.e., percentage land of a certain cover). Landscape configuration metrics measure the spatial distribution of patches within the landscape (i.e., degree of aggregation and contagion).

2.2. ECOSYSTEM FUNCTION

In ecology, *ecosystem function* is the ability of earth's processes to sustain life over a long period of time. Biodiversity is essential for the functioning and sustainability of an ecosystem. Different species play specific functions, and changes in species composition, species richness, and functional type affect the efficiency with which resources are processed within an ecosystem. Thus, the loss of species will impair the biogeochemical functioning of an ecosystem. Furthermore, the distribution, abundance, and dynamic interactions of species can be good indicators of ecosystem condition. Often the disappearance of species precedes changes in ecosystem function and overall health (Rapport et al. 1985). There are a variety of possible target species and measures of ecosystem function (i.e., energy flow, nutrient cycles, productivity, species interactions). Several scholars suggest that the single best index is net primary production (NPP), which determines the amount of sunlight energy fixed by the processes of photosynthesis to support life on earth.

The concept of ecosystem function has evolved over time to include the interactions between system's structure and functions and spatial heterogeneity (Likens 1998; Pickett et al. 2001; Alberti et al. 2003). Ecosystems are now seen as open, dynamic, unpredictable, and multiequilibria. In these systems, disturbance is highly frequent and succession can occur through multiple pathways. Resilience depends on the distribution, abundance, and dynamic interactions of species, at several spatial and temporal scales (Holling 2001; Peterson and Holling, 1998). In this framework, functional diversity should be the focus of biodiversity conservation, shifting the attention from individual species (Folke, Holling, and Perrings 1996). Since several species fill similar ecological roles, it is possible to maintain key-functions of the ecosystem in the face of change, by maintaining the distribution of redundant species across multiple time and space scales (Nystrom and Folke 2001).

To understand the dynamics and interactions between pattern and process in urban ecosystems requires the consideration of multiple scales of space, time, and organization. Urban landscapes exhibit distinctive spatial patterns at different scales, which may be caused by different processes operating at that scale. Urban landscapes can also be hierarchically structured. This requires a hierarchical patch dynamics modeling and scaling approach that deals explicitly with spatial heterogeneity, functional complexity, and multiplicity of scale across landscapes. Spatial patterns and ecological processes occur at multiple scales; thus, scale is key to understand their interactions (Wu and Qi 2000).

3. Linking Urban Patterns to Ecosystem Function

The question of how patterns of human settlements affect ecosystem function is becoming increasingly important in ecology (Collins et al. 2000; Grimm et al. 2000; Pickett et al. 2001). Humans increasingly dominate ecosystems. In Figure 1, I apply a conceptual model developed by Alberti et al. (2003) for studying urban ecosystems to analyze the impacts of urban patterns on ecosystem function. Changes in land cover affect biotic diversity, primary productivity, soil quality, runoff, and sedimentation rates. By altering the availability of nutrients and water, urban activities also affect population, communities, and ecosystem dynamics. Urbanized areas also modify the microclimate and air quality by altering the nature of the surface and generating large amount of heat. The urban heat island, which in turn serves as a trap for atmospheric pollutants, is perhaps the best-known example of inadvertent climate modification (Oke 1987). Furthermore, the increase in impervious land area associated with urbanization affects both geomorphological and hydrological processes causing changes in water and sediment fluxes (Wolman 1967; Leopold 1968; Arnold and Gibbons 1996; Paul and Meyer 2001). Since ecological processes are tightly interrelated with the landscape, the mosaic of elements

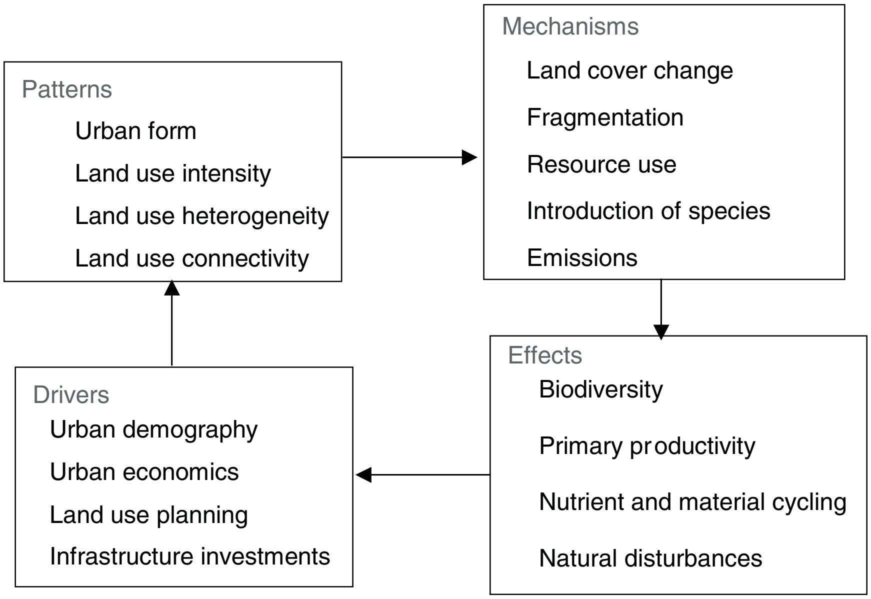

FIGURE 1. Effects of Urban Patterns on Ecosystem Function

Source: Application of conceptual model as proposed in Alberti et al. (2003).

resulting from urbanization has important implications for ecosystem dynamics. Patchiness is likely to be heavily influenced by land use.

Table 1 provides a summary of the current evidence on the effect of urbanization on ecosystem functions. Other reviews have addressed various aspects of ecology in cities and of cities (Pickett et al. 2001; Berkowitz, Nilon, and Hollweg 2002). The synthesis proposed here clearly reveals the gap in the study of urbanization patterns.

3.1. NET PRIMARY PRODUCTIVITY

Urbanization is a major driver of land conversion. Most important, it takes place on the most productive lands (Imhoff et al. 1997). Using a night lights footprint derived from DMSP/OLS satellite images and digital soils maps, Imhoff et al. (1997) estimated that urban areas occupy ~3 percent of the land area of the continental United States. But they also indicated that most of urbanization is taking place on the best soils—those with the fewest limiting factors. Urbanization in the United States occupies respectively 6, 48, 35, and 11 percent of the land in the high, moderately high, moderate, and low soil productivity categories. Urban-induced change in NPP—the rate at which primary biomass is created—differs from region

TABLE 1. Summary of Selected Findings on the Effects of Urban Patterns on Ecosystem Functions

Ecosystem Function	*Findings*	*References*
Primary productivity	Urbanization in the US has reduced the annual net primary productivity (NPP) by 0.04 Pg C or 1.6 percent of its preurban value	Imhoff et al. 2002
	Urbanization is taking place on the best soils	Imhoff et al. 1997
Biodiversity		
Vegetation and flora	Exotic species greater in urban and suburban oak-dominated stands in New York	Rudnicky and McDonnell 1989
	Native flora decrease from the urban fringe to the city core	Kowarik 1990
	Native species decreased from the urban fringe to the city core in several Latin American cities	Rapoport 1993
	Plant diversity is greater in larger patches in urban areas	Bastin and Thomas 1999
Birds	Urbanization alters the composition of urban avian communities (decrease native species and increase exploiters)	Beissinger and Osborne 1982; Mills, Dunning, and Bates 1989; Blair 1996; Bock, Bock, and Bennett 1997; Marzluff 2001
	Canyon habitat age, total area of chaparral, total area of canyon, and predation	Soulé et al. 1988
	Urbanization affects nest predation, brood parasitism, and food availability	Robinson and Wilcove 1994; Newton 1998
	Exotic generalists between 80 to 95 percent of bird community in cities	Wetterer 1997
	Proximity to urban land use influence bird communities in urban green spaces	Nilon and Pais 1997
	Cats and other domestic pets influence bird population in suburban areas	Churcher and Lawton 1987

(continued)

Table 1 (continued)

Ecosystem Function	*Findings*	*References*
Fish and invertebrates	Fish diversity decreased with increase in impervious surface	Klein 1979; Steedman 1988; Schueler and Galli 1992
	Effects of impervious surface on fish diversity is minimized in streams with high riparian vegetation	Yoder, Miltner, and White 1999
	Benthic Index of biotic integrity decrease with increase in impervious	Allan, Erickson, and Fay 1997; Yoder, Miltner, and White 1999
	Effect of impervious surface on biotic integrity is reduced when intact riparian zones	Horner et al. 1997
Nutrient and material cycles		
Biogeochemical processes	Cities have energy budgets 100 to 300 times greater than natural ecosystems	Odum 1997
	Higher phosphorus concentrations in basins with higher percent of urban land use	Omernik 1976; Meybeck 1998; Wernick, Cook, and Schreier 1998
	Mass loss and nitrogen release maximum in urban oak stands and N-mineralization highest in urban stands	Pouyat, McDonnell, and Pickett 1997
	Urban litter decomposition is slower than rural areas	Carreiro et al. 1999
	Concentration of heavy metals, organic matter salts, and soil acidity increase with proximity to the urban core	Pouyat, McDonnell, and Pickett 1995
	Hydrological processes Urbanization increases surface runoff	Arnold and Gibbons 1996
	Increase in bankfull discharge with increasing impervious areas	Booth and Jackson 1997
Geomorphology processes	Channel enlargement increases with increasing impervious surface	Hammer 1972

(continued)

Table 1 (continued)

Ecosystem Function	*Findings*	*References*
	Soil erosion increases catchment sediment yields	Wolman 1967; Leopold 1968
	Disturbance regimes Urban areas have high degree of invasive and immigrant species	McDonnell et al. 1997
	Human sources of disturbance include introduction of exotic species, modification of landforms and drainage networks, control or modification of natural disturbance agents and the extensive infrastructure	Pickett et al. 1997
	Vegetation in housing developments is subject to catastrophic disturbances when buildings are demolished and rebuilt	Sukkop and Starfinger 1999
	Suppressing disturbances alters landscape heterogeneity	Turner, Carpenter, and Gustafson 1998

to region based on the ecosystem surrounding a city. However, overall urban land transformation in the United States has reduced the annual NPP by 0.04 Pg C or 1.6 percent of its preurban value (Imhoff et al. 2002).

NPP is not only influenced directly by urbanization. Urban areas also affect primary productivity through the demand and appropriation of natural resources from distant regions. Rees and Wackernagel (1994) have proposed to quantify such impact in terms of what they defined the ecological footprint. The ecological footprint is the ecologically productive area needed to provide the ecological services necessary to support the human population (Folke, Johnson, et al. 1997; Folke, Kautsky, et al. 1998; Young et al. 1998; Jansson et al. 1999). The ecological footprint of Metro Toronto and Vancouver, for example, are estimated to amount respectively to about 181,260 (Onisto, Krause, and Wackernagel 1998) and 29,722 square kilometers (Rees 1996), which correspond to about 100 to 300 times their nominal area.

While the ecological footprint is a useful indicator of the impact that the human population have on earth ecosystems, it does not allow us to specify how alternative patterns of urban development differently affect primary productivity. Furthermore, since natural resources are not typically distributed uniformly across landscapes, Luck et al. (2001) used a spatial explicit approach to show that the location of urban areas and interurban competition may play a crucial role in determining the magnitude of the ecological footprint.

3.2. BIODIVERSITY

Fragmentation of natural patches is one of the best-known impacts of human activities on the diversity, structure, and distribution of vegetation (Levenson 1981; Ranney, Bruner, and Levenson 1981; Brothers and Spingarn 1992). Ecologists have described its opposite quality—*connectivity*—as a critical property of landscapes, which facilitates or limits the movement of resources and organisms among natural patches (Turner and Gardner 1991). Urban growth affects connectivity directly by modifying the landscape and indirectly by changing the biophysical structure. Ecological studies have established relationships between landscape structure and the distribution, movement, and persistence of species. Although the differential effect of alternative urbanization patterns on plants is still not fully understood, it is known that converting natural or rural landscape into an urbanized landscape reduces the diversity of native plant species in the urbanized region. The edge effect has also been studied particularly in forests (Ranney, Bruner, and Levenson 1981; Harris 1984; Brothers and Spingarn 1992; Murcia 1995). Because forests are primarily vertical in structure, the removal of vegetation, and the consequent exposure to natural and human disturbances, have important consequences on the structure and composition of plant communities.

Based on the physical changes observed on the urban-to-rural gradient (Pickett, Burch, et al. 1997; Pickett, Cadenasso, et al. 2001), McKinney (2002) described a biodiversity gradient with species richness declining from the urban fringe towards the urban core. Not only habitat is increasingly lost from the rural and toward the urban core, it is replaced by remnant, ruderal, and managed vegetation and built habitat with various degree of inhabitability for most native species. Species composition along this gradient is characterized by urban exploiters dominating the urban core, urban adapters dominating suburban areas, and urban avoiders dominating the urban fringe (Blair 2001; McKinney 2002).

Birds are excellent indicators of the effects urbanization has on ecosystems since they respond rapidly to changes in landscape configuration, composition, and function. Urbanization affects birds directly through changes in ecosystem processes, habitat, and food supply and indirectly through changes in predation, interspecific competition, and diseases (Marzluff, Gehlbach, and Manuwal 1998). Percentage of the land cover covered by vegetation is in fact a good predictor of the number of bird species. Urbanization alters the composition of urban avian communities by increasing the number of introduced species and drastically reducing the number of native species (Marzluff 2001). Native species decline in population because of reduced natural habitats and inability to tolerate human disturbances (Beissinger and Osborne 1982; Blair and Walsberg 1996).

Several studies of the impacts of urbanization on birds have started to explore how urban patterns affect bird survival (Beissinger and Osborne 1982; Bolger et al. 1997; Rolando, Pulcher, and Giuso 1997; Marzluff, Gehlbach, and Manuwal 1998). These studies document how urbanization modifies the composition of urban avian communities through change in climate, food and water supply, nest sites, and predators. Most studies have not asked directly questions on the effects of urban patterns, but instead they investigate how habitat fragmentation creates edges and reduces vegetative cover and their implications for food supply, nest placement, and predation. Beissinger and Osborne (1982) compared the avian community of a mature residential area in Oxford, Ohio, with two control sites in Hueston Woods State Park. The urban community supported nine fewer species than the forest, a difference explained primarily by reduction of vegetative cover and increased habitat patchiness. In a study of breeding bird diversity and abundance in Springfield, Massachusetts, Tilghman (1987) found that woodland size is the most important single variable explaining the number of bird species.

A more direct question related to habitat fragmentation in urban areas is addressed by Soulé et al. (1988) in a study of birds that require native chaparral in thirty-seven fragments of canyon habitat in coastal, urban San Diego. Focusing on the effect of isolation on species diversity, they found that four variables could explain 90 percent of the variation in species richness across the fragments: canyon age, total area of chaparral, total area of canyon, and predation. In addition, they found that the absence of coyotes in urbanized environments allowed greater numbers of gray foxes and other avian predators. By eliminating large predators, urbanization offset their capacity to control small predators and their impacts on birds. Furthermore, cats and other domestic pets influence bird population in suburban areas (Churcher and Lawton 1987).

Studies of the effect of habitat fragmentation on birds are extensive and provide evidence of the effects of various degrees of urbanization on community diversity and reproduction. However, it is not known how the variation in the concentration, intensity, heterogeneity, and connectivity of urban development influences abundance and community diversity of birds and their chance of reproduction and survival.

3.3. Material and Nutrient Cycles

The conversion of forests to developed land associated with urbanization affects nutrient cycling, soil erosion, hydrological flow, and the runoff of pollutants from urban areas. Disturbances in urban environments that change biogeochemical movements and transformations have been extensively studied. Several studies have pointed to new sources and pathways of nutrients across the urban landscape (Newcombe 1977). Recently, Baker et al. (2001) have tracked the human input of nitrogen in the Phoenix metropolitan area and indicated the important role of fertilizers, human food, fuels, and nitrogen oxides production by fossil fuel combustion.

Landscape position and spatial patterns affect both horizontal (i.e., nutrients in surface water) and vertical flows (carbon exchange between the atmosphere and biota). However, the effect of landscape structure on the redistribution of material and nutrients is much less known.

We know that urban development affects plant-environment interactions and vegetation functions. The urban forest influences the microclimate and the atmospheric concentration of pollutants and local carbon storage fluxes (Jo and McPherson 1995). McPherson et al. (1994) estimated that in 1991, the tree cover in Chicago removed 17 tons of CO, 93 tons of SO_2, 98 tons of NO_2, 210 tons of O_3, and 234 tons of (less than 10 micron) PM. These trees also store 942,000 tons of carbon. Among other important ecological functions of the urban forest include the mitigation of storm-water runoff and flood control. No less important is the role of urban vegetation in providing critical aesthetic values and community well-being. While the evidence provided in the literature substantiates the hypothesis that urban patterns affect plant communities and vegetation functions in urban ecosystems, studies not addressed how alternative spatial urban structures influence the ecosystem function of the urban forest.

Several studies have indicated that the percentage of impervious surface in urban watershed is a good predictor of its health (Paul and Mayer 2001). Fish and macroinvertebrates have been used to compare the biotic integrity of streams exposed to various degrees of urbanization in watersheds. The two taxonomic groups are used to measure both the biotic diversity and the pollution tolerance of species. Evidence from current studies documents the relationship between land use/land cover and biotic integrity. Because biophysical and biological processes influence fish stream dynamics, land use activities result in alterations in fish population and communities (Schlosser 1991). But while fish reflect conditions over a large scale, macroinvertebrates may better reflect local environmental conditions.

More recent studies have hypothesized that local land use and habitat variables are superior to regional land use in predicting biotic integrity (Richards, Johnson, and Host 1996; Lammert and Allan 1999). In a more recent research, the author together with an interdisciplinary research team has established that the spatial distribution of impervious area in the watershed and its connectivity to the channel affect the hydrologic response of the watershed and, thus, the biological conditions in a stream (Alberti et al. n.d.; see section 5.2 of this article). Alternative land use patterns have as a consequence differential effects on aquatic ecosystems.

3.4. *DISTURBANCE REGIMES*

Urban landscapes exhibit rich spatial and temporal heterogeneity. Landscape features in urban environment are typically characterized by sharp boundaries, mostly as the result of human activities. Spatial and temporal heterogeneity within an urban landscape has both natural and human sources. Natural sources of disturbance such as the physical and biological agents and disturbance regimes are modified by humans through the introduction of exotic species, modification of landform and natural drainage, and change in disturbances (Pickett and Rogers 1997; Zipperer et al. 2000).

Disturbances are discrete events that disrupt ecosystem structures and functions (Pickett and White 1985). In urban areas, the alterations of natural disturbance regimes, along with the introduction of invasive species, have altered natural succession. Several changes in disturbance regimes result from urban development. First, urban development rescales natural disturbances by reducing or increasing their magnitude, frequency, and intensity. It also rescales areas by introducing biogeographic barriers (roads, canals, etc.) and reducing natural vegetation patch size. In addition, urban development introduces new disturbances, chronic stresses, unnatural shape complexity, or degrees of connectivity. Furthermore, changes in patch structure and integration homogenizes natural patterns by changing land use and modifying the natural processes that maintain biodiversity.

Changes in land cover and land use can cause intense changes in disturbance regimes and drive fundamental changes in biodiversity and ecosystem function. Housing development, road building, urban wasteland, and landfills are only some of the most obvious source of these disturbances. Change in microclimate, hydrological patterns, morphology, soil conditions, and habitat indirectly modify natural disturbance regimes. However, as for the other categories of effects addressed above, the existing literature does not address how various patterns of housing and roads influence the extent, distribution, intensity, and frequency of disturbances.

4. AN EMPIRICAL STUDY IN THE PUGET SOUND

To illustrate the direction of research linking urban patterns to ecosystem function, I draw on an empirical study developed at the University of Washington Urban Ecology Research Laboratory: The Impact of Urban Patterns on Ecosystem Dynamics[2] (see Alberti et al. n.d.). The study aimed to empirically explore relationships between urban patterns and ecological conditions in the Puget Sound Region. We developed and tested formal hypotheses of how patterns of urban development affect bird communities and aquatic macroinvertebrates through changes in biophysical processes and what factors determine and maintain an urban ecological gradient. We investigated four questions:

1. How do variables describing urban landscape patterns vary on an urban gradient?
2. What pattern metrics best describe the composition and configuration of urban landscapes?
3. What is the relative importance of pattern metrics in predicting changes in ecological conditions?
4. At what spatial scales are various ecological processes controlled in urban landscapes?

Our overarching hypotheses stated that

1. Urban spatial patterns can be described along distinct dimensions that represent relationships between biophysical (land cover) and socioeconomic variables (land use).
2. Urban landscapes are complex pattern of intermixed high- and low-density built-up areas that can best be described using a series of pattern metrics that link urban development to ecological conditions.
3. The predictive ability of models that relate aggregated measures of urbanization to ecological processes can be improved by including patterns of urbanization.
4. The predictive ability of a model, which relates a pattern variable to an ecological process, varies with change in spatial scale (resolution and extent).

4.1. RESEARCH APPROACH

Ecological signatures of alternative development patterns in the Puget Sound metropolitan region are quantified using land use and land cover pattern metrics. Land use data at the parcel level were obtained from King and Snohomish County assessor office. Land cover data were interpreted from Landsat Thematic Mapper (TM) imagery for the Puget Sound region for 1998. The land cover classification procedure creates an eight-class land cover system that discriminates between three classes of urban land cover characterized by varying levels of impervious surface and vegetation coverage at 30 m resolution. These are *paved urban* (approximately 100 percent paved cover), *grass/shrub urban* (characteristic of newer suburban areas with limited tree canopy and relatively large lawn coverage), and *forested urban* (characteristic of mature residential neighborhoods with a high degree of canopy cover). In addition, the procedure discriminates among three types of nonurban vegetation (*grass/shrubs/crops*, *deciduous forest*, and *coniferous forest*) and *water* (Hill, Botsford, and Booth 2002).

We applied six landscape metrics to measure urban landscape patterns: percent land (PLand), mean patch size (MPS), contagion, Shannon index, aggregation index (AI), and percent of like adjacencies (PLADJ). Details on the spatial metrics and methodology are in Alberti et al. (n.d.). Percentage land is the sum of the area of all patches of the corresponding patch type divided by total landscape area. Mean patch size is the sum of the areas of all patches divided by the number of patches. The Shannon diversity index represents the number of land use classes in the landscape. Contagion, AI, and PLADJ all measure various aspects of aggregation of the land cover.

Percent of paved land, percent of mixed urban, percentage grass, percentage forest, Shannon, contagion, slope, and distance from the central business district are used to discriminate six aggregated land development patterns including single family residential (SFR), mixed use, commercial, office, and open space. Percent of paved land, percent of mixed urban, and contagion are the best discriminant for the six types. We used these landscape patterns to assess their relationships between urban development and ecological conditions, specifically aquatic macroinvertebrates and avian diversity.

To establish relationships between urban patterns and aquatic invertebrate study, we delineated forty-two subbasins of variable degree of urbanization from forty-two points with an associated Benthic Index of Biological Integrity (B-IBI). B-IBI is an index of biotic integrity developed by James Karr at the University of Washington. We chose basins that were not larger than 5km^2. We developed five scales of analysis for investigation with each spatial metric. From large-scale analysis to small-scale analysis these scales are basinwide scale, 300m riparian zone, 200m riparian zone, 100m riparian zone, and local riparian zone.

The study of avian diversity is based on fifty-four 1km^2 study areas randomly selected in the Puget Sound region. We stratified the area by dominant land cover (forest, urban, urban forest), mean size of urban patches, and pattern of forest-settled area contagion. We restricted our selection to low (<500m) elevation sites dominated by coniferous forest (details of metrics and selection approach are in Alberti, Botsford, and Cohen 2001). At each study site, we measured bird relative abundance during the breeding season (2000-2001).

4.2. SUMMARY OF RESULTS

We describe complex relationships between land use and land cover in urban landscapes as revealed by the distributions of land cover across parcels with different land uses (Figure 2). Using various percentages of land cover types, we were able to discriminate across the different land use parcels. Our study shows that SFR parcels have significantly lower amount of impervious surface than multifamily parcels. We also find a great percentage of impervious surface on mixed-use parcels, where a combination of residential and commercial activities are located, and on industrial parcels. On the other hand, a high percentage of forest cover is found in SRF, while this drops significantly in the other development types. Our results also show high variability of land cover composition within land use types. We find that parcel size, location of the parcel over an urban to rural gradient, and year built influence significantly the distribution of land cover within land use types. More important, the results show that land development types have different land cover signatures both in terms of amount and level of fragmentation of natural land cover that can be preserved under different land use scenarios.

We established empirical relationships between metrics of landscape patterns and a series of stressors of aquatic ecosystems in the selected subbasins using stepwise multiregression models (Alberti et al. n.d.). The study clearly indicates that not only amount of impervious surface but also patterns of urban development and roads are correlated with ecological conditions. Best individual predictors of B-IBI are number of road density ($R^2 = .67$, $p < .001$) and road crossings ($R^2 = .68$, $p < .001$). We also showed that landscape configuration measured as mean patch size, aggregation index, and percent adjacency of urban and forest patches explain the variability of B-IBI not explained by percent of impervious area: AI

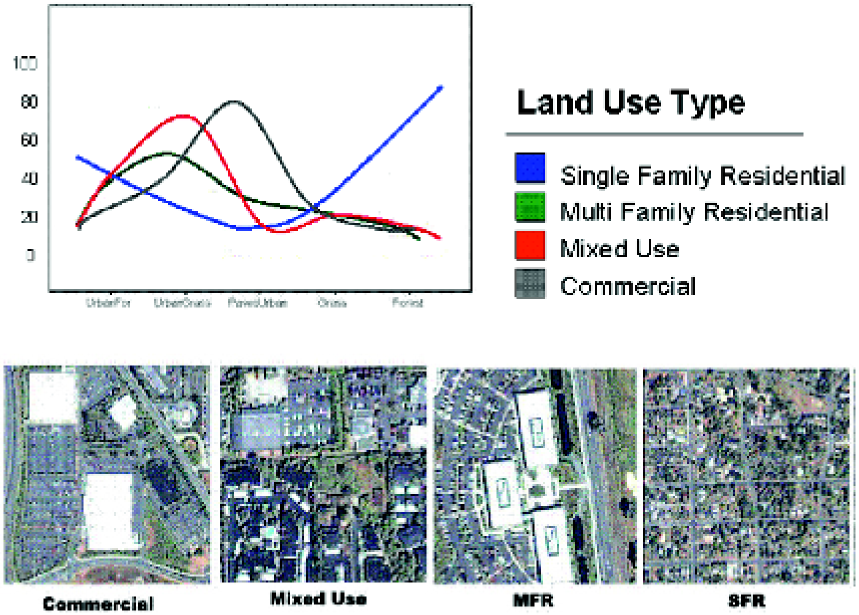

FIGURE 2. Distribution of Land Cover across Land-Use Types

forest ($R^2 = .65$, $p < .001$), MPS urban ($R^2 = .64$, $p < .001$), AI urban ($R^2 = .63$, $p < .001$) and PLADJ forest and PLADJ urban ($R^2 = .63$, $p < .001$). In addition, percentage impervious area and percentage forest have an R^2 of .61 and .59, respectively ($p < .001$). Together MPS of paved land and road crossing explain the variance in B-IBI (Alberti et al. n.d.).

Finding for the avian study indicated that fewer species occur within forest fragments ($M = 14.9$, $SE = 0.60$) than in settled areas ($M = 25.0$, $SE = 0.61$; $n = 40$ sites with forest and settlement; paired $t_{(39)} = 13.1$; $p < .0001$). The amount of forest patch in the developed area was significantly correlated with bird diversity. The number of bird species increased with increasing amount of forest while the arrangement of forest in the area was less important than the total amount. Bird diversity remained high in the settled Puget Sound region if the percentage of forest in each 100 ha unit remained at ~30 percent or more. In our study sites, this happened despite variation in forest connectivity (measure by the forest aggregation index). It is not surprising that connectivity, or interspersion of forest and settlement, mattered less to birds in a region with a vast forest matrix.

5. IMPLICATIONS FOR FUTURE STUDIES

In this article, I have suggested that explicitly linking urban patterns to ecosystem function is critical to advance urban ecological research and to develop strategies to minimize impacts of urban growth. Current ecological research already provides increasing evidence of the impact of urbanization on ecosystem function. But it simplifies the consideration of urban structures to such an extent that the results are not useful to urban planners and managers. Furthermore, it fails to recognize the complex interactions between urban pattern and ecological processes that occur across multiple scales. To understand how species populations and community characteristics change in response to urban development, we need to expand our knowledge about drivers and effects of ecosystem structure and functions in urban landscape.

Building on the existing evidence provided by the urban planning and landscape ecology literature, it is possible to articulate testable hypotheses on the mechanisms that link urban patterns to ecological function. Particularly, we can start to systematically test hypotheses linking urban development patterns to patch structure in urbanizing landscapes and their consequences for primary productivity, biodiversity, nutrient, and material cycles and disturbance regimes. We can ask, for example, what degree of concentration or dispersion of the urban structure best allows urban landscapes to maintain the integrity of patch structure. We can also investigate how land use intensity and urban pattern interact to affect ecological conditions. For example, we can investigate how modification of the landscape structure (i.e., amount of impervious surface and vegetation) at a subwatershed scale interact with local effects of the land use on the riparian zone. Moreover, we can establish what role transportation and surface water artificial drainage infrastructures play in the overall impact.

It is clear from the current knowledge, however, that the interactions between urban economic, social, and ecological processes are extraordinarily complex.

Interactions between urban patterns and ecosystem function are controlled by multiple stressors. We will need to investigate relationships between urban patterns and human-induced stressors, interactions among multiple stressors associated with these patterns, and the existence of thresholds in these relationships. Results from current research also indicate that these human-ecological interactions are process specific. To assess the impacts of alternative patterns of urban development and determine their trade-offs, we need to consider that diverse species play different roles in ecosystem processes. We also need to consider that dynamics interactions between urban patterns and ecosystem function occur at multiple spatial and temporal scales. The concepts of target species and functional diversity provide a new framework for studying the impact of urban patterns on ecosystem function and for designing more effective conservation strategies. Particularly, it suggests the importance of establishing the degree of redundancy—multiple species per functional group—necessary to maintain urban ecosystem sustainability over the long term.

NOTES

1. United Nations estimates and projections adopt national definitions of urban centers incorporated in the last census, which may differ between countries. The United Nations defines "urban agglomeration" as the population contained within the contours of a contiguous territory inhabited at urban levels without regard to administrative boundary.

2. "The Impact of Urban Patterns on Ecosystem Dynamics," principal investigator, M. Alberti; co–principal investigators, D. Booth, K. Hill, and J. Marzluff.

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