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Ecological resilience in urban ecosystems: Linking urban patterns to human and ecological functions

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Abstract. Urban ecosystems evolve over time and space as the outcome of dynamic interactions between socio-economic and biophysical processes operating over multiple scales. The ecological resilience of urban ecosystems—the degree to which they tolerate alteration before reorganizing around a new set of structures and processes—is influenced by these interactions. In cities and urbanizing areas fragmentation of natural habitats, simplification and homogenization of species composition, disruption of hydrological systems, and alteration of energy flow and nutrient cycling reduce cross-scale resilience, leaving systems increasingly vulnerable to shifts in system control and structure. Because varied urban development patterns affect the amount and interspersion of built and natural land cover, as well as the human demands on ecosystems differently, we argue that alternative urban patterns (i.e., urban form, land use distribution, and connectivity) generate varied effects on ecosystem dynamics and their ecological resilience. We build on urban economics, landscape ecology, population dynamics, and complex system science to propose a conceptual model and a set of hypotheses that explicitly link urban pattern to human and ecosystem functions in urban ecosystems. Drawing on preliminary results from an empirical study of the relationships between urban pattern and bird and aquatic macroinvertebrate diversity in the Puget Sound region, we propose that resilience in urban ecosystems is a function of the patterns of human activities and natural habitats that control and are controlled by both *socio-economic* and *biophysical processes* operating at various scales. We discuss the implications of this conceptual model for urban planning and design.

Keywords: aquatic macroinvertebrates, birds, fragmentation, land cover, resilience, urban sprawl, urbanization

Introduction

The environmental changes associated with urbanization have been significant during the last century and are expected to continue through the next several decades. Urban development fragments, isolates, and degrades natural habitats (Marzluff, 2001), simplifies and homogenizes species composition (Blair, 2001), disrupts hydrological systems (Arnold and Gibbons, 1996; Booth and Jackson, 1997), and modifies energy flow and nutrient cycling (McDonnell and Pickett, 1990; Medley *et al.*, 1995; McDonnell *et al.*, 1997; Vitousek *et al.*, 1997; Grimm *et al.*, 2000). Urbanized area accounts only for ∼1 to 6 percent of the total earth surface (Meyer and Turner, 1992), but cities appropriate a large share of earth's carrying capacity in terms of resource input and waste sinks (Rees, 1996). Cities import ecological services from distant regions and depend on the ecological transformations that occur on the global scale. Changes in ecological conditions associated with urbanization—such as the contamination of watersheds, loss of biodiversity, and change in climate—affect local and global ecosystem services and ultimately their ability to sustain the urban population and its infrastructure operating on a global scale.

In this paper we explore ecological resilience in urban ecosystems—the degree to which they can tolerate alteration before reorganizing around a new set of structures and processes (Holling, 1973, 1996). We use the term "resilience" to refer to the size of the basin of attraction around a stable state, which defines the maximum perturbation that can be tolerated by the system without causing a shift to an alternative stable state. We propose that in urbanizing regions complex interactions between human and ecosystem functions over multiple scales affect resilience. These complex interactions need to be included in studying such systems. Simply considering human and ecosystem functions separately may not be adequate to understand system resilience because integrated socio-economic and ecological systems can behave differently than their separate parts. Furthermore, since urban development patterns affect the amount and pattern of built and natural land cover, as well as human use of ecosystem services in urban ecosystems, we argue that alternative urban patterns (i.e., urban form, land use distribution, and connectivity) have differential effects on resilience.

We build on urban economics, landscape ecology, population dynamics, and complex system science to propose a conceptual model that explicitly links the urban pattern to the human and ecosystem functions, and therefore resilience, in urban ecosystems. Although many competing models have addressed the relationship between urbanization and ecosystem function (Collins *et al.*, 2000; Grimm *et al.*, 2000; Pickett *et al.*, 2001), few have directly asked the question of how human and ecological patterns emerge from the interactions between socio-economic and biophysical processes. Nor have they investigated how these patterns control the distribution of energy, materials, and organisms in human-dominated ecosystems. We do not know, for example, how clustered versus dispersed and monocentric versus polycentric urban patterns emerge and how differently they affect ecological change. Our focus is on building a theory amenable to formal testing of the relationships between urban patterns and ecological resilience. Drawing on preliminary results from an empirical study of the impact of urban patterns on bird (Donelly and Marzluff, 2004) and aquatic macroinvertebrate diversity (Alberti *et al.*, in review) in the Puget Sound region, we propose that resilience in urban ecosystems is a function of the patterns of human activities and natural habitats. We do not measure resilience directly, but draw on the hypothesized correlation between biotic diversity and resilience to better link our empirical and theoretical ideas. We discuss the implications of this conceptual model for urban planning and design.

Complexity in urban ecosystems

Urban ecosystems evolve over time and space as the outcome of dynamic interactions between *socio-economic* and *biophysical* processes operating over multiple scales (Alberti, 1999a). From these complex interactions emerge an ecology in which humans are dominant agents (Collins *et al.*, 2000; Grimm *et al.*, 2000; Pickett *et al.*, 2001; Alberti *et al.*, 2003). As in other complex adaptive systems, patterns at higher levels emerge from localized interactions acting at lower levels (Levin, 1998). Cities are prime examples of emergent socioeconomic and ecological phenomena (Alberti *et al.*, 2003). Patterns of traffic congestion, pollution, and sprawl are the outcome of multiple local interactions and feedback mechanisms between human decisions and ecological processes in urbanizing regions. Individual choices and actions taken by many agents—households, businesses, developers, and governments affect ecosystem processes and ecological conditions, which in turn control human decisions.

An essential aspect of complex systems is nonlinearity, which leads to multiple possible outcomes of dynamics (Levin, 1998). Urbanizing regions have multiple steady and unstable states. In urbanizing regions, urban sprawl leads to the shift from a natural steady state of abundant and well-connected natural land cover to a second steady state of greatly reduced and highly fragmented natural land cover (figure 1). The exact form of the natural "steady" state depends on natural disturbance regimes. The sprawl state is a forced equilibrium that relies on incomplete information regarding the full ecological costs of providing human services to low-density development. Sprawl is a state that is unstable because it is based on importing ecosystem services from other areas. The state of an urban ecosystem is likely driven between natural and sprawl states by the amount of urbanization (figure 2). We define these states as the natural vegetation and the sprawl attractors, where the system eventually ends up. The steady state of abundant and well-connected natural land cover is

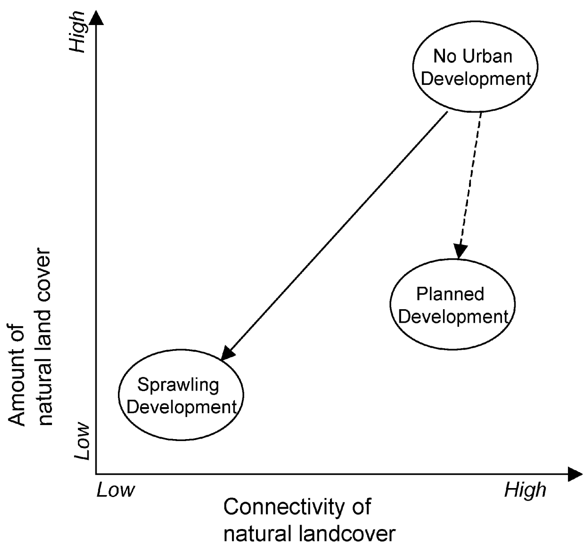


Figure 1. Steady states and transitions in urbanizing environments. Natural disturbance regimes maintain relatively stable arrangements of amount and connectivity of natural land cover when human presence is minimal. (In our example a temperate forest system with long return intervals between disturbances is envisioned.) With a lack of information and consideration only of short-term gains, the natural trajectory is for provision of human services to drive the system to sprawl where little natural land cover remains. A "driven equilibrium" of sprawling development results. Planning and consideration of benefits of natural land cover to human services can force a different equilibrium that simultaneously supports humans and other species in urban ecosystems. However, this forced equilibrium has very low resilience because provision of ecosystem services pulls it toward the natural steady state and provision of human services pulls it toward the sprawl state.

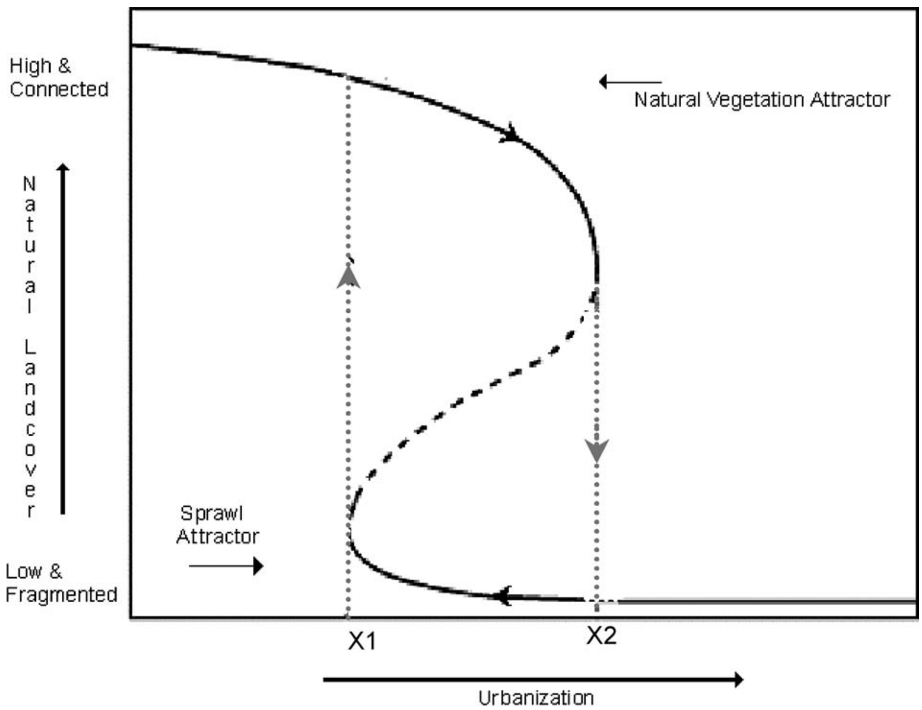


Figure 2. As urbanization increases, natural vegetation decreases. The system moves along the upper solid line (Natural vegetation attractor) until a point (X_2) is reached where natural vegetation is too degraded and fragmented to perform vital ecological services and the system becomes unstable (dashed portion of curve). As urbanization reduces ecosystem function the system flips into a sprawl state (the lower solid line, Sprawl attractor) where human services replace ecosystem services. Eventually ecosystem services are degraded to a point that cannot support human services, urbanization declines and the system becomes unstable again (X_1). The system eventually returns to the natural vegetation state.

what we define the natural vegetation attractor. The sprawl attractor is characterized by a highly fragmented landscape, increasing substitution of ecological functions with human functions and highly reduced capacity of ecological function to support human function.

As urbanization increases, the system shifts from the natural vegetation attractors and sprawl attractors. The system moves away from the natural vegetation attractor toward the sprawl attractor and beyond, until increasing urbanization reduces the ability of ecological systems to support the human population. We hypothesize that the replacement of ecosystem services with human services in urbanizing regions over the long term, eventually reaches a threshold when it drives ecosystems to collapse. This process drives the system back toward the natural vegetation attractor if ecosystem collapse reduces settlement to the point that substantial natural vegetation can regrow. Our hypothesis assumes a time scale of centuries or millennia. Many large human settlements have collapsed in the past possibly because the local environment was extensively degraded or the ecological carrying capacity changed in response to large scale climatic shifts (i.e. cities built and abandoned by the Mayas, Anasazi, the Incas, and the Egyptians).

Interactions within and between urbanization and ecological and human functions involve several feedback mechanisms. Within urban development, real estate markets involve feedback mechanisms of buyer and seller adjusting prices in reaction to relative abundance or scarcity of real estate. Feedback mechanisms can be negative, or dampening forms that tend to stabilize systems such as real estate markets, or alternatively may be positive forms of feedback, accelerating adjustments and leading to unstable conditions that change catastrophically as in the case of ecological succession or extinction of species. The switch between the multiple states is often abrupt and the system response to perturbation is highly non-linear and complex. The non-linearity arises from the strong interactions between multiple agents and competition between the natural vegetation and urban development for space. The characteristic response shows strong hysteresis, that is when the ecosystem state shifts from the vegetation state to the sprawl state, it becomes highly resistant to switching back.

Sprawl and natural vegetation states have important and differential effects on humans and ecological components of urban ecosystems. The typical effect of urban sprawl is to reduce and degrade natural land covers by conversion, fragmentation, perforation, and appropriation (Medley *et al.*, 1995; Buechner and Sauvajot, 1996; Theobald *et al.*, 1996; Marzluff, 2001) leaving systems less resilient to transition from wholly natural to wholly anthropogenic land cover. Urban sprawl also increases the per capita costs of human services and infrastructure provision (Ewing, 1994). To balance these effects and allow urban ecosystems to provide both human and ecosystem services, urban planners must devise patterns of human settlement that are in the state region that is inherently unstable. The challenge is to increase the resilience of unstable states to attraction of either sprawl or natural vegetation steady states where only human or ecosystem services, respectively, are provided.

Although extensive research is increasingly focusing on the interactions between humans and ecological systems, the diverse urban processes have yet to be synthesized into one coherent conceptual model. Both ecologists and social scientists still study various components of urban ecosystems separately. As a result, urbanization is seen as the process by which humans substitute ecosystem services (e.g., watershed purification) with human services (e.g., wastewater treatment plants). To illustrate this perspective, various states of ecosystems at various stages of urbanization from no human settlement to highly urbanized can be represented in relation to ecosystem services and human services (figure 3). In this view, urbanization leads to a decline in ecosystem services and increase in human services. Pristine environments, on the other hand, maintain high ecosystem services but only indirectly provide human services. However, this view assumes that ecosystem services and human services are maintained by a set of independent ecological and economic processes. In reality, ecosystem services directly provide human services in non-urbanized areas and indirectly support human services in urbanized ones (Daily, 1997). Urban areas import ecosystem services from vast areas. Eventually, human services in urbanized areas decline as ecosystem services locally and globally are reduced by the increasing pressure posed by urbanization. The functional form of the relationships between ecosystem and human services and urbanization depends on each service being considered (figure 4).

Assessing the resilience of urban ecosystems requires understanding how interactions between humans and ecological processes affect the resilience of inherently unstable

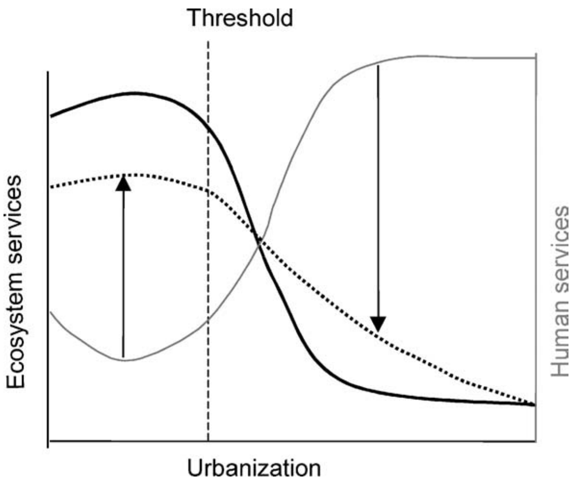
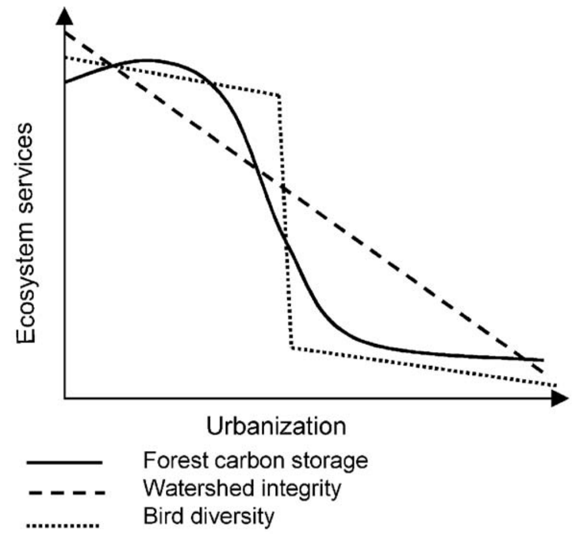


Figure 3. The two lines in black and gray represent a partial view of the relationship between urbanization and ecological and human services. Urbanization is measured in developed land per unit area. The line in black indicates a decline in ecological service as a result of urbanization. The gray line indicates the substitution of ecological services with human services. This view assumes that ecological and human services are independent. However, there is a threshold between urbanization and ecological conditions after which ecological services collapse. The dotted line represents an integrated view of the combined ecosystem and human services. Ecosystem services directly provide human services in non-urbanized areas and indirectly support human services in urbanized ones. Eventually human services in urbanized areas decline as ecosystem services are reduced by urbanization.

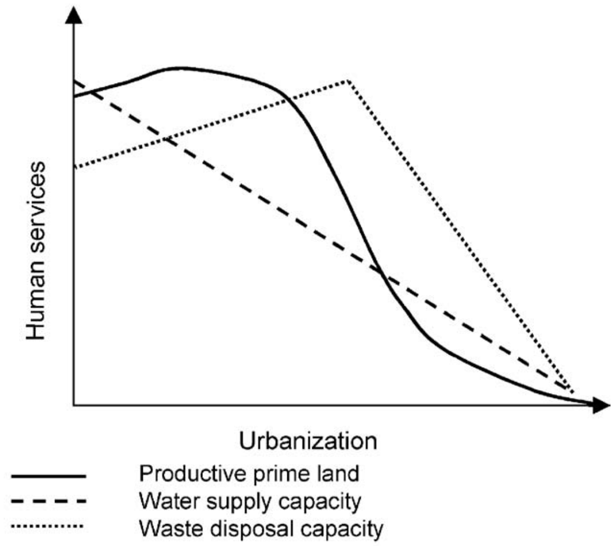
equilibrium points between the natural vegetation attractor and the sprawl attractor. In other words, understanding how to best balance human services and ecosystem services in urban ecosystems. Ecosystem services are the processes and conditions that sustain humans and other species (Daily, 1997). Human services in urban areas such as housing, water supply, transportation, waste disposal, and recreation depend on ecosystems for natural resources and their productivity over the long term. They also depend on the ecosystem's ability to act as a sink to absorb emissions and waste. Ecosystems also provide other important services to the urban population: they regulate climate, control flooding, and absorb carbon, to mention a few (Ehrlich and Mooney, 1983; Daily, 1997; Costanza *et al*., 1997). Human services depend on both local and global ecosystem services because cities import resources from distant areas. On the other hand, the ability to maintain such services both locally and globally increasingly depends on human activities and the development patterns of human settlements.

Linking human and ecosystem functions: A conceptual model

In studying the interactions between humans and ecological processes in urban ecosystems we need to consider that many factors work simultaneously at multiple scales (Alberti, 1999a). Urban ecosystems consist of several interlinked subsystems—social, economic,



a) Examples of ecosystem services



b) Examples of human services

Figure 4. The two figures (a and b) represent stylized representations of functional relationships between (a) ecosystem services and urbanization and (b) human services and urbanization.

institutional, and ecological—each representing a complex system of its own and affecting all the others at various structural and functional levels. Many small changes in system patterns at one level can create system instability and unpredictable events at another. On the basis of hierarchy theory, Pickett *et al.* (1994) argue that the consideration of interactions only at the upper level may provide statistical relationships but cannot help explain or predict important feedback for future conditions. We hypothesize that this is particularly true in urban ecosystems because urban development controls ecosystem structure in complex ways. Land use decisions affect species composition directly through the introduction of species and indirectly through the modification of natural disturbance agents and land cover. Production and consumption choices determine the level of resource extraction and generation of emissions and wastes. Decisions about investing in infrastructures or adopting control policies may mitigate or exacerbate these effects. Since ecological productivity influence the regional economy, interactions between local decisions and ecological processes at the local scale can result in large-scale environmental change.

We develop a conceptual model to assess the resilience of urban ecosystems by integrating multiple-scale social and ecological processes into a common framework (figure 5). We hypothesize that a set of biophysical and human agents drives urban socio-economic and biophysical patterns and processes that control ecosystem functions. Without an accurate description of how spatial and temporal patterns of human activities affect and are affected by ecosystem function, one can neither test hypotheses about the systems' dynamics

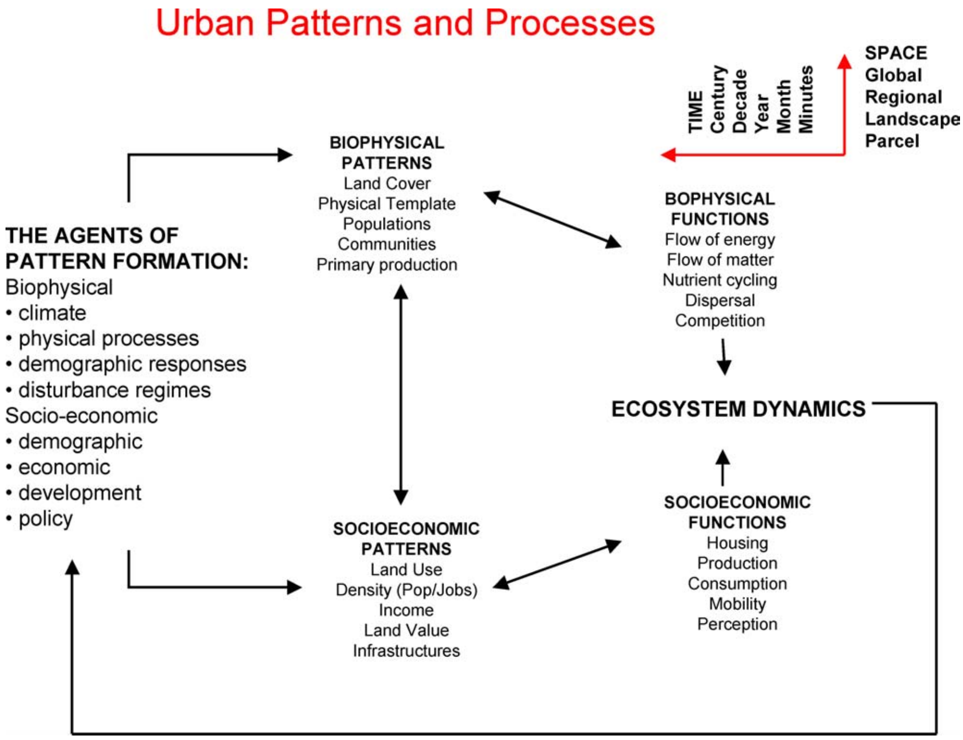


Figure 5. Biophysical and socio-economic patterns are driven by the interactions of multiple biophysical and socio-economic agents and affect ecosystem dynamics through biophysical and socioeconomic functions over multiple temporal and spatial scales. Examples of functions are listed: They are not exhaustive.

nor produce reliable predictions of ecosystem change under different human-disturbance scenarios. This conceptual model provides the theoretical basis to generate and test formal hypotheses about the mechanisms that link urban patterns and ecosystem dynamics at multiple scales and their influence on the resilience in urban ecosystems.

According to the theory of adaptive cycle, dynamic systems do not tend toward some stable condition (Gunderson *et al.*, 1995; Holling *et al.*, 2002). Instead they follow four characteristic stages: rapid growth (r), conservation (K), collapse (Ω), and renewal and reorganization (α) (Carpenter *et al.*, 2001). In urbanizing regions the progression proceeds from the exploitation phase (r) to the conservation phase (K) when urban population growth leads to unchecked growth and urban sprawl. The progression from the phase r to K (conservation) is when patterns reinforce and the system becomes more rigid. An example is the effect of road infrastructure on the landscape pattern. The effect is both direct through increased development and indirect through the effects on the real estate market. Resilience in this phase decreases as the stability domains contract. The system becomes more vulnerable to surprises. The Ω phase is characterized by rapid collapse or release, that follows the effects of rapid growth and its ecological consequences. This is followed by a phase of reorganization (α), during which new policies are developed. In the succeeding r phase, the system changes its trajectory (Gunderson *et al.*, 1995; Carpenter *et al.*, 2001; Gunderson and Holling, 2001).

In urbanizing regions, urban sprawl (phase K) leads to the movement from a natural steady state of abundant and well-connected natural land cover to a second steady state of greatly reduced and highly fragmented natural land cover (figure 1). Clearly ecosystem services are greatly reduced at the stable equilibrium characterized by extensive urban sprawl (McDonnell *et al.*, 1997; Vitousek *et al.*, 1997; Dobson *et al.*, 2001; Costanza *et al.*, 2002; Hansen *et al.*, 2002). However, human services may also be compromised in sprawling development because of increased infrastructure costs and the effect of reduced ecosystem services on human services in the long term (Frank, 1989). Due to the lack of feedback (e.g., results of decisions on highway development), this can lead to a rapidly collapsing dynamic (Phase Ω). Feedback is phase-lagged often by decades and returns to decision makers and actors in unexpected forms that are often not obviously causally connected. For the most part, residents in the suburban periphery have not confronted the full costs of providing public services (e.g., utilities) in sprawled areas of the city (Ottensmann, 1977). Often municipalities' provision of services subsidize sprawl since services are priced independent of their real cost and distance from central facilities (Ewing, 1994, 1997).

In response to the human, ecological, and economic costs of sprawling development, urban planning has attempted to stabilize inherently unstable states—ones that balance conversion of natural land cover with development needed to support human services. The assumption of planned development is that the development pattern affects ecological conditions and the maintenance of ecosystem and human functions. In the phase of reorganization and renewal (phase α), urban ecosystems have a chance to change trajectory toward the development of self-organizing processes of interacting ecological and socio-economic functions. This forced equilibrium is inherently unstable, as it requires balancing tension between provisioning human and ecosystem services. Nature pushes against this balance point to return to a steady state defined by natural disturbance regimes. People informed

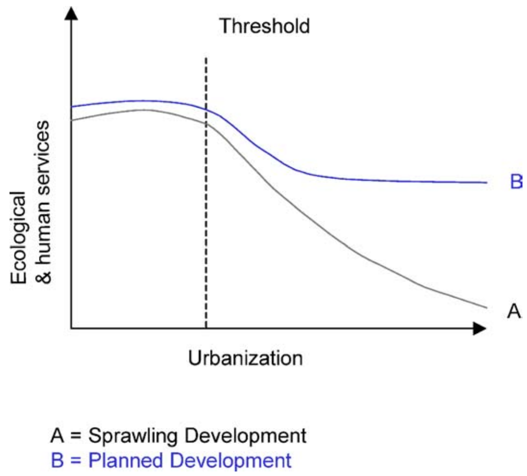


Figure 6. Relationships between urban patterns and ecosystem and human services. Human and ecosystem services are interdependent. Alternative urbanization patterns have different levels of resilience measured as their capacity to simultaneously support ecological and human services. Sprawling development (A) will lead to reduced ecosystem services and ultimately will affect human services. Planned development (B) is an urban development pattern that maintains the conditions for simultaneously supporting ecological and human services.

only with shortsighted economic forecasts push against it to return to a state of sprawl. The trajectory the system will take depends strongly on information flows, knowledge transfer, and system learning. In urban ecosystems foresight, communication, and technology (Holling *et al.*, 2001) enhance the capability of information flows to control system dynamics and feedback mechanisms and provide increased opportunities for innovative response to ecological crises. This makes it possible to increase resilience of a planned equilibrium.

One key element of such information is the resilience of alternative urban development patterns in terms of their ability to simultaneously maintain ecosystem and human functions over the long term (figure 6). Resilience of alternative urban patterns changes with the system functions being considered. A steady state of abundant and well-connected natural land cover cannot simultaneously maintain ecosystem and human functions, nor can a greatly reduced and highly fragmented one. Resilience of alternative patterns also depends on the temporal and spatial scale. Indeed, resilience can be achieved in one time period at the expense of the future, and at one scale at the expense of a broader scale (Carpenter *et al.*, 2001). Designing resilient development patterns requires an understanding of the mechanisms that link urban patterns to human and ecosystem functions at multiple spatial and temporal scales.

Relating urban pattern to ecological resilience: A hypothesis

The hypothesis that the spatial configuration of development in an urban region influences ecosystem dynamics has been debated for some time (Lynch, 1960; Godron and Forman, 1982; Turner, 1987; Steinitz, 1990; Forman, 1995; Alberti, 1999b). It is based on the idea that the spatial patterns of the urban setting alter the biophysical structure and habitat and influence the flows of resources. Various configurations of the urban structure imply alternative outcomes in terms of the amount and interspersion of the built and natural land cover that have differential effects on ecological processes. Urban patterns affect resource flows directly by redistributing solar radiation and mineral nutrients and indirectly by determining the resources needed to support human activities. Urban patterns also influence the feasibility of using alternative systems to supply resources and services to the urban population, thus indirectly affecting their environmental impact (Alberti, 1999b).

Urban landscapes exhibit rich spatial and temporal heterogeneity. Natural sources of heterogeneity include the biological and physical agents, the disturbance regime, and stresses (Pickett and Rogers, 1997). The human sources 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 *et al.*, 1997). Landscape ecologists have started to document the impact that various arrangements of patch structure have on ecosystems (Godron and Forman, 1982; Turner, 1989; Forman, 1995; Collinge, 1996). From an ecological perspective, urban development produces a variety of unprecedented and intense disturbances through physical changes in the landscape (Forman and Godron, 1986; Turner, 1989; Holling, 1992; Wu and Loucks, 1995). First, it rescales natural disturbances by reducing or increasing their magnitude, frequency, and intensity. In addition, urban development introduces new disturbances, chronic stresses, biogeographic barriers, unnatural shapes and degrees of connectivity. Finally it homogenizes natural patterns by changing land use and modifying the natural processes that maintain diversity.

Spatial heterogeneity in urbanizing regions also affects the level of environmental pressure that individuals exert (Alberti and Susskind, 1997). The effect of a household or business on the land depends on location and density of development. Housing the same number of people requires variable amounts of land development and infrastructure depending on land development choices. Whether an urban dweller chooses a private or public transportation system to commute between home and work depends, among other considerations, on the availability of an efficient public transportation system and the economic feasibility of such systems given the pattern of development. Similarly the development patterns influence both the demand and cost of infrastructure to provide a variety of human services from transportation to water and wastewater and thus the amount of ecosystem services required to support them.

The relationship between type of land development and cost of water and wastewater infrastructure provides a good example of the complex interactions between the form of urbanization and the ability to provide human services. The demand for water in the US can be as high as 700 liters per day per person but varies substantially across units depending on the development type among single family detached (1,215 l/day), single family attached (799 l/day), and multifamily (617 l/day) housing (NRC, 2000). Similarly sewer demand varies as a function of development type among single family detached (973 l/day), single family attached (719 l/day), and multifamily (587 l/day) housing. The cost of providing such infrastructure not only increases with the varying demand of alternative development types, it also depends on its location on a rural to urban gradient. Utility provision costs per unit range respectively for water and sewer for single family detached housing from \$2,000 and \$4,300 in rural areas to \$1,600 and \$3,200 in suburban areas and \$1,310 and \$2,810 in urban center (NRC, 2000). The implications of these figures are that housing the same number of people in the form of urban sprawl costs more in terms of water and sewer infrastructure provisions. Based on these figures, a recent study on the Cost of Sprawl by the National Research Council (NRC, 2000) estimates that nationwide residential and nonresidential growth between 2000 and 2025 will require an additional local water and sewer capacity for the daily provision of more than 36.3 billion liters of water and the treatment of more than 32.1 billion liters of sewage per day. By comparing an uncontrolled and a controlled growth scenario, the study shows a difference and a saving in costs of more than \$12 billions over the 25 year time period (NRC, 2000).

To be effective, a conceptual model of urban ecosystems requires an explicit representation of the relationships between spatial heterogeneity and human and ecosystem processes. Such an approach is essential to understanding how spatial heterogeneity is created within landscapes and how that heterogeneity influences the flow of energy, matter, species, and information across the urban landscape. While several scholars have extensively described the urban landscape as a mosaic of biological and physical patches within a matrix of infrastructure, social institutions, cycles, and order (Machlis *et al.*, 1997), few have explored the interactions between biophysical and human sources (Pickett *et al.*, 2000). We believe that these interactions control the mechanisms that link spatial heterogeneity to human and ecological processes and their influence to ecosystem dynamics. Using this framework we can ask questions about how urban development patterns affect ecological function and resilience in urban ecosystems. Ecosystem function is an important driver of the state of urban ecosystems (figure 2). As ecosystem function declines, the system transitions from natural vegetation to sprawl steady states. If ecological function declines substantially at high levels of urbanization, the system may return to an unstable state again.

An empirical study in the puget sound region

To illustrate our argument linking urban patterns to ecological resilience, we draw on an empirical study currently being developed at the University of Washington: The impact of urban patterns on ecosystem dynamics[1] (Alberti *et al.*, 2004). The study seeks to empirically explore relationships between urban patterns and ecological conditions in the Puget Sound region. While the empirical study is limited to the ecosystem function and ecological resilience of an urbanizing region, we build on the literature to link the ecological and human function through the patterns of development. In the study, we develop and test 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 investigate 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? And (4) at what spatial scales are various ecological processes controlled in urban landscapes?

Land use and land cover

Methods. Urban ecological gradients in the Puget Sound metropolitan region are quantified using land use and land cover pattern metrics. Researchers in landscape ecology have developed a large number of metrics for quantifying such patterns and their effects on disturbance regimes (Turner *et al.*, 1989). We applied six metrics to measure urban landscape patterns: percent land (Pland), mean patch size (MPS), contagion (C), dominance (D), aggregation index (AI), and percent like adjacencies (PLADJ). 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. We used the Geographic Resources Analysis Support System (GRASS) to estimate Pland, MPS, Contagion and Dominance (Baker, 1997). The percent of land cover occupied by each patch type (i.e. paved land, forest, or grass) is considered an important indicator of ecological conditions since some ecological properties of a patch can be influenced by the composition of the patches and abundance of similar patches within the landscape. Percent 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. Contagion is the probability that two randomly chosen adjacent cells belong to the same class. This is calculated by the product of two probabilities: the probability that a randomly chosen cell belongs to category type i, and the conditional probability that given a cell is of category type i, one of its neighboring cells will belong to a different type. Dominance is the deviation from the maximum possible landscape diversity given a number of land cover types contained in the landscape. We also quantify landscape configuration using AI and PLADJ indices with Fragstats (McGarigal *et al.*, 2002). AI equals the number of like adjacencies involving the corresponding class, divided by the maximum possible number of like adjacencies of that class. PLADJ equals the sum of the number of like adjacencies for each patch type, divided by the total number of cell adjacencies in the landscape; and multiplied by 100 (to convert to a percentage). Percentage values were arcsin-square root transformed prior to analysis.

Results. Complex relationships between land use and land cover are revealed by the distributions of land cover across parcels with different land uses (figure 7). Different land use parcels can be discriminated using different land cover classes. Single-family residential parcels have significantly lower amount of impervious surface than multifamily parcels, although these parcels may accommodate a much larger number of households. Even greater is the percentage of impervious surface on mixed-use parcels where residential and commercial activities are located in industrial parcels. On the other hand a high percentage of forest cover is found in single family residential parcels while this drops significantly in the other development types. Land cover composition varies much within the same land use types. This depends on parcel size, location of the parcel over an urban to rural gradient, and year built.

We also examined the relationships between land cover composition and configuration with land use in 42 drainage basins (Alberti *et al.*, in review). The percentage of impervious area in these basins is highly correlated with the percentage of transportation use ($R^2 = 0.88$,

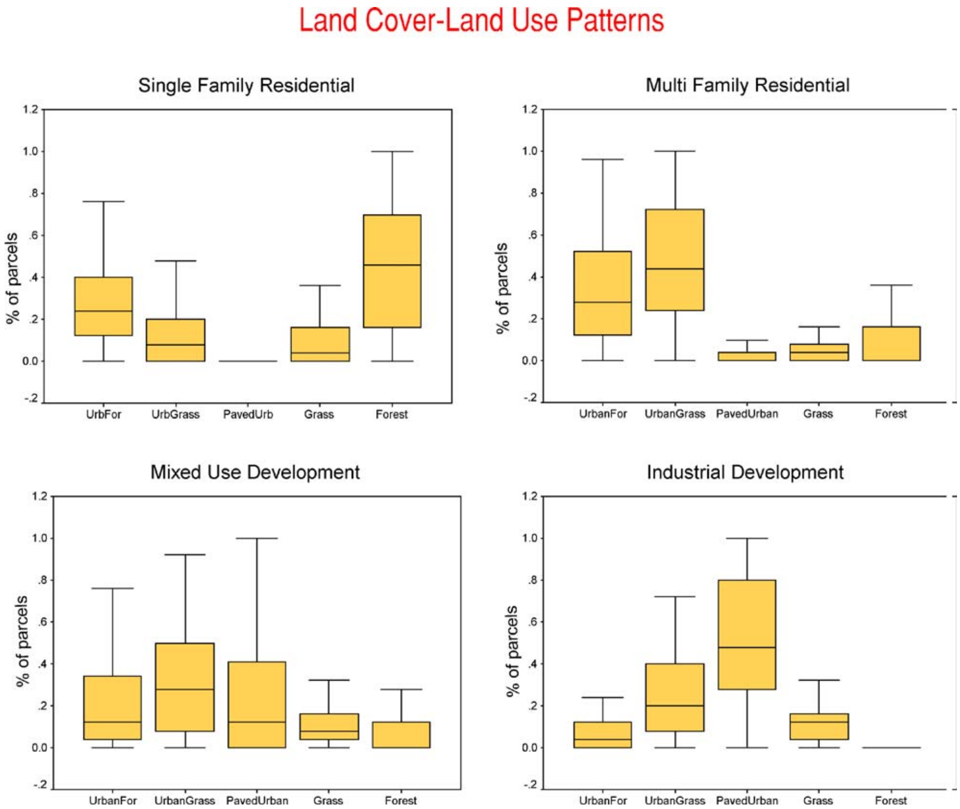


Figure 7. Distributions of land cover across parcels with different land uses in King County. Land use data are extracted from assessor data associated with individual parcels. The land cover classification discriminates between five classes including forest, grass, and three classes of urban land cover characterized by varying levels of impervious surface and vegetation coverage. These are: paved urban (>60% paved cover), grass/shrub urban (>20% and <60% paved and >25% grass) and forested urban (>20% and <60% paved and >25% forest).

$P < 0.001$), population density ($R^2 = 0.84$, $P < 0.001$) and housing density ($R^2 = 0.79$, $P < 0.001$). Our findings also show that 95 percent of the variation in aggregation of urban paved land measured by the aggregation index could be explained by four variables including: Percent transportation ($R^2_{(\text{adjusted})} = 0.78$, $P < 0.001$), open space ($R^2_{(\text{adjusted})} = 0.91$, $P < 0.001$), population density ($R^2_{(\text{adjusted})} = 0.87$, $P < 0.001$) and housing density ($R^2_{(\text{adjusted})} = 0.95$, $P < 0.001$).

Discussion. Urban ecological gradients in the Puget Sound metropolitan region can be quantified using land use and land cover pattern metrics: percent land, mean patch size, contagion, and dominance. The pattern metrics selected are useful to describe the composition and spatial configuration of urban development. Our regression models indicate that land uses, housing density, and the parcel position on an urban to rural gradient are good predictors of land cover composition and configuration. These results show that land development patterns have different impacts on the amount of natural land cover that can be preserved and level of fragmentation that will be generated under different land use scenarios.

Aquatic Macroinvertebrates

Methods. We delineated 42 subbasins of variable degree of urbanization from 42 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 (Karr, 1991). We chose basins that were not larger than five km^2. We developed five scales of analysis for investigation with each spatial metric. From large-scale analysis to small-scale analysis these scales are: basin-wide scale, 300 m riparian zone, 200 m riparian zone, 100 m riparian zone, and local riparian zone.

We establish empirical relationships between metrics of landscape patterns and a series of stressors of aquatic ecosystems in the selected subbasins using step-wise multi-regression models. We use the Geographic Resources Analysis Support System (GRASS) to calculate spatial metrics at 150×150 m and 900×900 m scale of analysis: entropy, Shannon index, richness, and Mean Patch Size. To calculate configuration metrics we reclassified land cover by collapsing forested urban, grass urban, interurban, and bare together; forest was left as the second class. Grass and water were masked out using r.mask. The sampling units were set to first calculate using a 150 m window, and a second analysis was done at 900 m. Shannon, richness, mean patch size, and entropy were calculated at both resolutions. The basin and basin portion grids were intersected with the 150 m grid. The intersection DBF files are then imported into SPSS, and case summaries of contagion, Shannon index, and mean patch size (mean and median for each) are computed. We calculated The AI and PLADJ indices using Fragstats (McGarigal *et al.*, 2002). A standard analysis type was used, with the 8-cell neighbor option.

Results. The findings of our study indicate significant statistical relationships between urban landscape patterns—both amount and configuration of impervious area and forest patches—and ecological conditions in streams (Alberti *et al.*, in review). The best individual predictors of BIBI were: road density ($R^2 = 0.67$, $P < 0.001$), # of road crossings ($R^2 = 0.66$, $P < 0.001$), AI forest ($R^2 = 0.65$, $P < 0.001$), MPS urban ($R^2 = 0.64$, $P < 0.001$), AI urban ($R^2 = 0.63$, $P < 0.001$), PLADJ forest ($R^2 = 0.63$, $P < 0.001$), PLADJ urban ($R^2 = 0.63$, $P < 0.001$), percentage TIA ($R^2 = 0.61$, $P < 0.001$), MPS forest ($R^2 = 0.60$, $P < 0.001$), and percentage trees ($R^2 = 0.59$, $P < 0.001$). The results from our apriori models show that MPS of paved land and road crossing together (R^2 of 0.70 $p < 0.001$) do a much better job than percent TIA alone (R^2 of 0.61 $p < 0.001$) in explaining the variance in B-IBI (Alberti *et al.*, in review).

Discussion. The study clearly indicates that at the scale of the watersheds supporting individual tributary streams, patterns of urban development affect ecological conditions on an urban to exurban gradient. At this scale, previous research has shown that impervious surfaces result in characteristically altered and often extreme hydrologic conditions that provide an endpoint on a disturbance gradient (Meyer *et al.*, 1988; Booth and Jackson, 1997; Konrad and Booth, 2002). We confirm that percent impervious surface does explain a great part of the variance in B-IBI across the sub-basins (figure 8a), but show that other variables that describe the configuration and connectivity of the landscape such as mean patch size and number of road crossing do a better job. The percent of impervious area and percent of forest in the contributing watershed are only coarse predictors of biological conditions in streams. The location and spatial configuration of both forest patches and paved areas explain most of the variability in BIBI (figure 9).

Avian diversity

Methods. We selected 54 one km^2 study areas in the Puget Sound region using a stratified random approach. We stratified the area by dominant land cover (forest, urban, urban forest), mean size of urban patches (contiguous settlement), and pattern of forest-settled area interspersion (contagion). We restricted our selection to low (<500 m) elevation sites dominated by coniferous forest. We randomly selected 2/4 replicates within existing combinations of these three attributes (details of metrics and selection approach are in Alberti, 2001; Donnelly, 2002; Rohilla, 2002). Within each site that was not entirely forest or settlement ($n = 40$), we studied birds in the settled and forested portions separately using six and two sampling points, respectively.

At each study site we measured relative bird abundance during the breeding season (2000/2001; one year per site; eight, 50-m fixed radius survey points per site; four visits per point per year from April to July (Ralph *et al.*, 1993)), persistence of individuals (resighting of marked birds), and reproductive performance (netting, spot mapping, nest searching; Christoferson and Morrison, 2001). These techniques are appropriate for visible or vocal species with relatively small home ranges. Therefore, we excluded large raptors and woodpeckers from our analysis and only report on occurrence of 56 species of migratory and resident birds. Here we present a community-level analysis only of species richness. Population and community responses are detailed in Donnelly and Marzluff (2004 and in review).

Results. We counted 10–37 species of birds at each site. Fewer species were detected within forest fragments ($x = 14.9$, SE= 0.60) than in settled areas ($x = 25.0$, SE= 0.61; $n = 40$ sites with forest and settlement; paired $t_{(39)} = 13.1$; $P < 0.0001$).

The amount of forest remaining in a development, not its arrangement, was significantly correlated with bird diversity. The number of bird species increased with increasing amount of forest regardless of whether we sampled the settled, forested, or total area of the 1 km^2 sampling area (figure 8b). Birds were counted separately in settled portions of the area, remaining forested portions, and totaled across the entire area. Diversity increased non-linearly with forest in the settled portions ($R^2_{\text{(adjusted)}} = 0.085$, $F_{(1,53)} =$

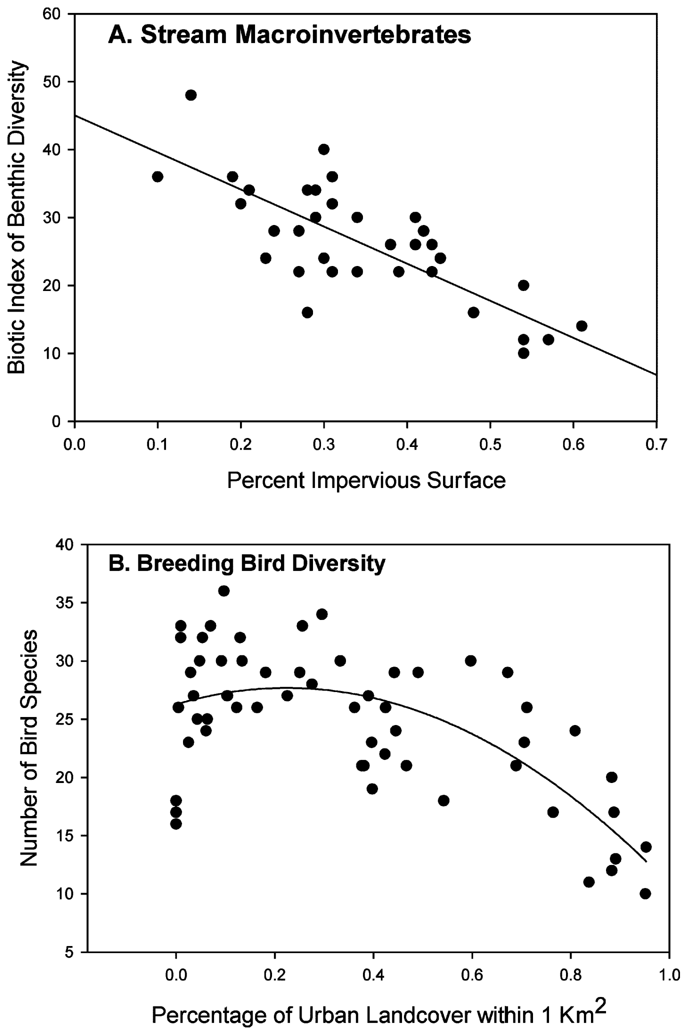
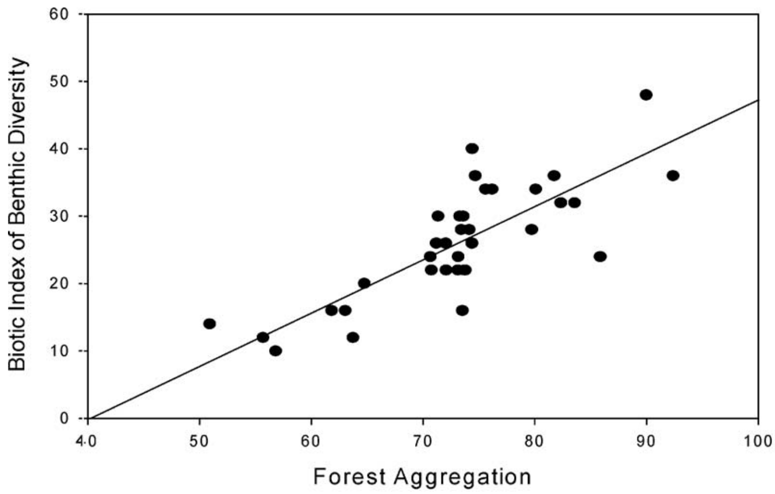


Figure 8. Relationship of benthic index of biotic integrity (A) and bird diversity (B) to percentage of the one km^2 study area that was forested. (A) B-IBI decrease linearly with increase in percent impervious area ($R^2 = 0.61$, $P < 0.001$). (B) Diversity increased non-linearly with forest in the settled portions ($R^2_{(adjusted)} = 0.085$, $F_{(1,53)} = 5.95$, $P = 0.02$) and for the total area ($R^2_{(adjusted)} = 0.26$, $F_{(1,53)} = 18.7$, $P < 0.001$). Least-squares regression lines are plotted with 95% confidence intervals. Analyses were done on transformed (arcsin-square root) percentages.

5.95, $P = 0.02$) and for the total area ($R^2_{(adjusted)} = 0.26$, $F_{(1,53)} = 18.7$, $P < 0.001$). In the forested portion, diversity increased linearly with proportion of the forest in the landscape ($r^2_{(adjusted)} = 0.12$, $F_{(1,53)} = 8.2$, $P = 0.006$). Least-squares regression lines are plotted with 95% confidence intervals. Analyses were done on transformed (arcsin-square root) percentages. The arrangement of forest in the area was less important than



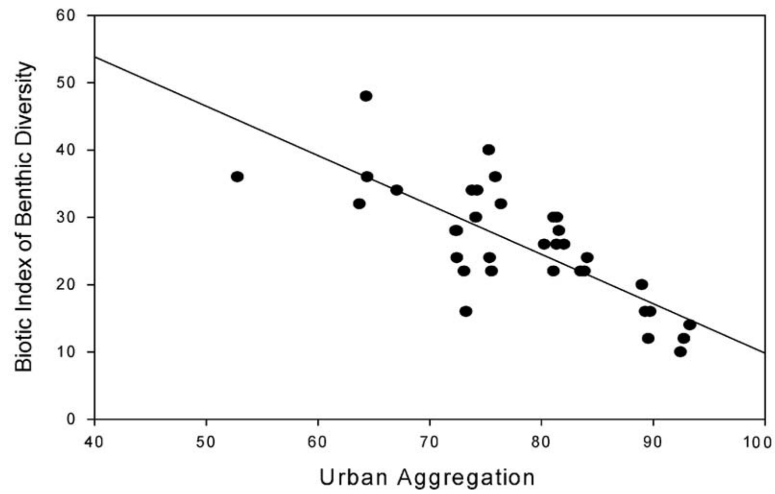


Figure 9. Relationship between landscape configuration (Aggregation index of Forest and Urban Land) and the Biotic Index of Biotic Integrity. B-IBI increases linearly with increase in the aggregation of the forst cover AI forest ($R^2 = 0.66$, $P < 0.001$) and decreases linearly with the aggregation of paved urban land AI urban ($R^2 = 0.60$, $P < 0.001$).

the total amount. An index of forest aggregation did not enter ($P = 0.14$) multiple regression models for species richness after percentage of forest was included. Moreover, regardless of amount of forest retained in a settlement, forest aggregation was at most weakly correlated with bird richness (figure 10).

Discussion. Bird diversity remained high in the settled Puget Sound region if the percentage of forest in each 100 ha unit remained at ~30% or more. In our study sites this happened

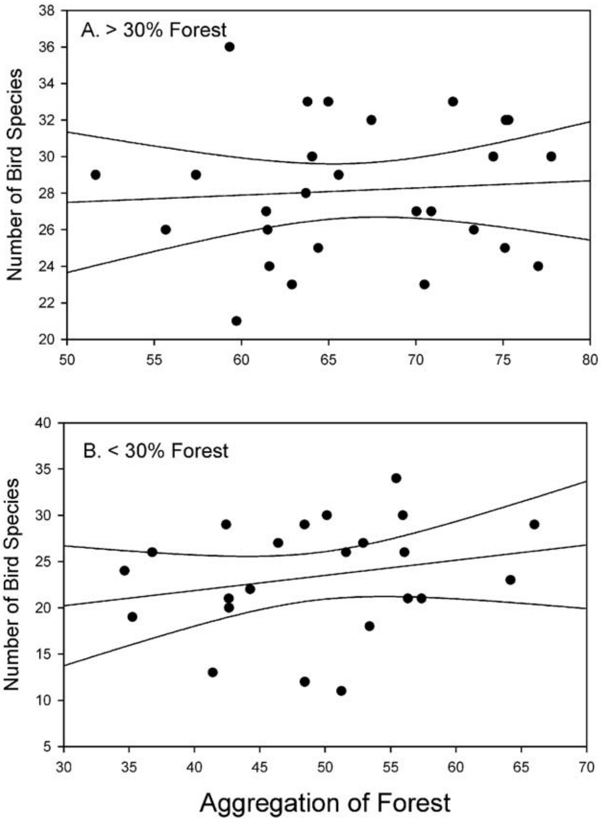


Figure 10. Relationship of bird diversity in sites with greater (A) or less (B) than 30% forest to aggregation of forest (proportion of forested pixels that were adjacent to other forest). Least squares regression lines and 95% confidence intervals are shown. Neither regression is significant (A: $r^2_{(\text{adjusted})} = 0.001$; $F_{(1,25)} = 0.14$, $P = 0.91$; B: $r^2_{(\text{adjusted})} = 0.04$; $F_{(1,25)} = 0.70$, $P = 0.42$).

despite variation in forest connectivity (measured by the forest aggregation index). It is not surprising that connectivity, or interspersion of forest and settlement, mattered less to birds in our region than absolute amount of forest. Our region is characterized by relatively high forest cover, much in protected reserves; 67% of the land cover in our study area was forest in 1998. Mobile birds appear able to easily disperse from these areas throughout any moderately forested areas despite human settlement.

The lack of importance of forest connectivity requires two caveats. First, forest coverage and aggregation are positively correlated. Our study areas having >30% forest cover also had >50% aggregation (50% probability that one pixel of forest was next to another pixel of forest). In a less aggregated study area, loss of connectivity may be detrimental, even to mobile species like birds. Second, here we only discuss overall species richness. Some species respond strongly and negatively to increasing interspersion. These forest interior specialists were relatively rare in our study (e.g., Winter Wren, *Troglodytes* troglodytes, (Linnaeus, 1758), Wilson's Warbler *Wilsonia pusilla* (Wilson, 1811), Swainson's Thrush, *Catharus ustulatus*, (Nuttall, 1840)). They may, however, be of more conservation concern or more critical to system resilience than the more common species that appear to benefit from interspersion of settled and forested areas (e.g., Steller's Jay, *Cyanocitta stelleri,* (Gmelin, 1788), Black-capped Chickadee, *Pollile atricapillus* (Linnaeus, 1766), Northern Flicker, *Colaptes auratus* (Linnaeus, 1758), and American Crow, *Corvus brachyrhynchos* (Brehm, 1822)) .

Bird diversity, stream integrity, and the resilience of urban ecosystems

In this study we do not measure resilience directly, but draw on the hypothesized correlation between biodiversity and resilience to develop hypotheses on the relationships between urban patterns and ecosystem resilience. Resilience of biological systems is difficult to define and to measure (Karr and Thomas, 1996; Carpenter *et al.*, 2001). We focus our analysis on biological diversity because species perform diverse ecological functions and ecologists have proposed that an increase in species richness also increases functional diversity (Tilman *et al.,* 1996) and resilience (Peterson *et al.,* 1998). We investigate the relationship between these measures and percent urban land cover in the landscape (figure 8a and b).

The stream study focused on macroinvertebrates as biological endpoints as the most integrative measures of river health (Karr, 1991). Stream biota has the full range of elements (i.e. species, assemblages) and processes (i.e. mutation, biotic interactions, nutrient dynamics etc.) that represent the system health (Karr, 1991, 1996). We show a linear relationship between urbanization and biotic integrity in streams. However, percent impervious area and percent forest in the contributing watershed is only a coarse predictor of biological conditions in streams, in part because hydrological change is only one of several factors that affect stream biota. The location and spatial configuration of forest patches and paved areas explain most of the variability in B-IBI not explained by TIA. While the processes of urbanization are correlated to stream degradation, they are by no means homogenous or uniform in terms of their explicit spatial patterns or implications to ecosystem functioning. Our empirical study shows that both the amount and configuration of impervious area and forest patches influence ecological function in streams and might influence their resilience.

We also focus our analyses on bird species diversity because diversity is thought to be correlated positively with ecosystem services (Loreau, 2000) and resilience (Naeem, 2002). However, this may not be the case in human-dominated ecosystems such as we studied. The reason that bird diversity was higher at the urban fringe rather than in forested areas was because many synanthropic species colonize settled areas in response to novel nesting and foraging opportunities provided by humans (Marzluff, 2001). This increased diversity is rather disturbance-specific and may not indicate the system's resilience to other perturbations. Conversely, because many modern and historical perturbations in our region (logging, fire, windstorms, etc.) reduce forest structure and create some of the conditions found in settlements (clearings, young forests, increased alder), bird communities in landscapes characterized by a mixture of settled and forested lands may indeed be more resilient than less diverse communities typical of extreme of no settlement (the presumably more stable equilibria). In this respect, the forced equilibrium resulting from informed urban planning may produce resilient, diverse bird communities characterized by mixtures of native forest birds and synanthropic colonists.

Conclusions

Urban ecosystems provide unique opportunities to test hypotheses about interactions between humans and ecological processes. In this paper we have argued that these complex interactions control ecosystem dynamics and need to be explicitly accounted for in order to assess the ecological resilience of urban ecosystems. We also need to consider that dynamic interactions between urban patterns and ecosystem function occur at multiple spatial and temporal scales. Thus, multiple scales should be considered in assessing these interactions. Because urban development patterns affect spatial heterogeneity of urban ecosystems, we have argued that alternative urban patterns that emerge from human and ecological interactions play an important role in the dynamics and resilience of urbanizing regions.

We develop a conceptual model to assess the resilience of alternative urban development patterns in terms of their ability to simultaneously provide ecosystem and human services over the long term. How urban patterns affect these functions is not known. Although many studies have addressed the relationship between urbanization and aspects of ecosystem function, few have asked directly how urban patterns control the distribution of energy, materials and organisms in urban ecosystems. 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, percent of impervious surface). However these metrics are only coarse predictors of biological conditions and do not discriminate between different landscape patterns. As such, they can offer only a limited suite of planning or management responses.

Preliminary results from our study of the effects of urban patterns on bird diversity and aquatic macroinvertebrates in the Puget Sound region show the complexity of these interactions. First we show that patterns of land use are not directly correlated with land cover. Urbanization results in a complex pattern of intermixed high- and low-density built-up areas. Urban land cover patterns cannot be derived directly from land use. Rather, they can best be described using a series of urban pattern metrics: some describe spatially aggregated variables (e.g., density of human population, road denisity or amount of impervious surface), some describe spatial distributions of land cover types.

They also indicate that these interactions are process-specific. Strong statistical relationships are found between selected landscape patterns—both amount and configuration of impervious area and forest patches—and ecological conditions in streams suggesting that patterns of urban development matter to watershed function. This relationship does not indicate a specific threshold but shows that both the increase in percentage impervious surface and its aggregation have a direct impact of stream macroinvertebrates. In particular, as the probability of paved areas being adjacent rises from 50 to 100, BIBI values decline from 50 to 10. A reverse relationship is found between aggregation of forest cover and BIBI.

Interspersion of forest and developed land mattered less to birds in our region than absolute amount of forest. Bird diversity remained high in the settled Puget Sound region if percentage of forest in each 100 ha unit remained at ∼30% or more. Both these results indicate that landscapes characterized by a mixture of settled and forested lands may indeed be more resilient than states of either abundant and well connected natural land cover or areas of extensive sprawl, neither of which can simultaneously maintain ecosystem and human functions.

These results indicate that patterns of urbanization are critical in balancing the tension between providing human and ecological services and maintaining the unstable equilibrium created by planned development. They also indicate that ecosystem responses vary with various ecological processes and that thresholds may exist. This knowledge is critical to determine what processes need to be maintained in order to ensure that urban ecosystem services can simultaneously support both humans and other species.

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Note

1. The Impact of Urban Patterns on Ecosystem Dynamics, Alberti M (PI), Co-PIs Booth, D., Hill, K. and J. Marzluff.

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