Integrating Humans into Ecology: Opportunities and Challenges for Studying Urban Ecosystems

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Our central paradigm for urban ecology is that cities are emergent phenomena of local-scale, dynamic interactions among socioeconomic and biophysical forces. These complex interactions give rise to a distinctive ecology and to distinctive ecological forcing functions. Separately, both the natural and the social sciences have adopted complex system theory to study emergent phenomena, but attempts to integrate the natural and social sciences to understand human-dominated systems remain reductionist—these disciplines generally study humans and ecological processes as separate phenomena. Here we argue that if the natural and social sciences remain within their separate domains, they cannot explain how human-dominated ecosystems emerge from interactions between humans and ecological processes. We propose an integrated framework to test formal hypotheses about how human-dominated ecosystems evolve from those interactions.

Keywords: ecology, human-dominated ecosystems, urban patterns, emergence, niche

For most of human history, the influence of human beings on biophysical processes, ecological systems, and evolutionary change has been relatively limited, as compared with the influence of "natural" (nonhuman) processes. Ecological and evolutionary change has generally been attributable to natural variation in energy and material flows and to natural selection by parasites, diseases, predators, and competitors. Today, however, humans affect Earth's ecosystems at extraordinary rates through conversion of land and resource consumption (Turner et al. 1991), alteration of habitats and species composition (McKinney 2002), disruption of hydrological processes (Arnold and Gibbons 1996), and modification of energy flow and nutrient cycles (Vitousek et al. 1997a, Grimm et al. 2000). Humans now use approximately 40% of global net primary production (Vitousek et al 1986) and more than half of accessible freshwater runoff (Postel et al. 1996). At least half of the world's forests have disappeared as a result of human activity, and three-quarters of that total have disappeared since 1700 (Harrison and Pearce 2001). Human activities fix amounts of nitrogen and sulfur comparable to those fixed by all nonhuman causes (Graedel and Crutzen 1989). Humans have radically revamped Earth's carbon cycle (Prentice et al. 2001) and freed into the environment vast quantities of naturally occurring trace materials (e.g., cadmium, zinc, mercury, nickel, arsenic) and exotic new anthropogenic substances (e.g., polychlorinated biphenyls, chlorofluorocarbons) (Pacyna and Pacyna 2001).

Humans also influence evolutionary processes. Selection is more and more frequently directed by people, or at least by people interacting with other natural processes. For example, humans affect speciation by challenging bacteria with antibiotics, poisoning insects, rearranging and exchanging genes, creating and dispersing thousands of synthetic compounds, and selectively fishing (Palumbi 2001). By hunting, moving predators and competitors around the globe, and massively reconfiguring the planet's surface, humans have increased extinctions of other species to levels 1000 to 10,000 times higher than those resulting from nonhuman causes (Pimm et al. 1994, Vitousek et al. 1997b, Flannery 2001). The combined effect of changing speciation and extinction is rapid evolutionary change (Palumbi 2001).

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Despite dominating Earth's ecosystems, humans remain conspicuously excluded as subjects of much ecological thinking and experimentation. Traditional ecological research investigates ecosystems in terms of biophysical, ecological, and evolutionary processes unaffected by human influences. During the last 100 years, formidable strides have been made in the scientific understanding of ecological systems (Likens 1998). Evolutionary theory and population genetics have made fundamental changes in the assumptions underlying ecological research. Ecological scholars no longer regard ecosystems as closed, self-regulating entities that "mature" to reach equilibria. Instead, they see such systems as multi-equilibria, open, dynamic, highly unpredictable, and subject to frequent disturbance (Pickett et al. 1992). In the newer non-equilibrium paradigm, succession has multiple causes, can follow multiple pathways, and is highly dependent on environmental and historical context. Ecosystems are driven by processes (rather than end points) and are often regulated by external forces (rather than internal mechanisms). The new ecological paradigm recognizes that humans are components of ecosystems (McDonnell and Pickett 1993). Yet ecological scholars often fail to include humans in ecological science (Hixon et al. 2002, Reznick et al. 2002, Robles and Desharnais 2002).

Applied ecology has extensively challenged the assumptions of an ecological paradigm that assumes human-free systems, but ecology has not yet provided a new theoretical framework to fully integrate humans into ecosystem studies. Here we argue that humans must be explicitly incorporated into all aspects of ecological thought, because, by adding powerful selection forces at every spatial scale and at many temporal scales, humans are fundamentally changing the expression of the rules that govern life on Earth. To paraphrase Hutchinson (1965), humans are changing the ecological stage on which the evolutionary play is performed. To understand the new evolutionary play, ecological scholars must build a new stage with humans as a central plank.

Urban ecology: Understanding human-dominated ecosystems

Planet-scale changes induced by humans are most evident in and around the urbanizing landscape (figure 1). Urbanized areas cover only approximately 1% to 6% of Earth's surface, yet they have extraordinarily large ecological "footprints" and complex, powerful, and often indirect effects on ecosystems. Earth's urban population has increased more than 10-fold over the past century, from 224 million in 1900 to 2.9 billion in 1999 (Sadik 1999). According to the United Nations (Sadik 1999), all expected population growth from 2000 to 2030 (approximately 2 billion people) will be concentrated in urban areas. By 2030, more than 60% (4.9 billion) of the estimated world population (8.1 billion) will live in cities.

Ecological scholars studying urban areas have challenged ecological theory to explain the ecology in and of cities (Pickett et al. 2001). The urban long-term ecological research sites are now producing important empirical observations (Collins et al. 2000). Some have argued that important revisions to ecological theory are needed to include human activity (Collins et al. 2000, Grimm et al. 2000). To understand specific sets of interactions between humans and ecological processes that occur in urbanizing regions, we propose examining cities as emergent phenomena—phenomena that cannot be explained simply by studying the properties of their individual parts. Cities are both complex ecological entities, which have their own unique internal rules of behavior, growth, and evolution, and important global ecological forcing functions.

Cities as emergent phenomena. Ecology is a science of emergent phenomena: Populations have properties (birth and death rates) and behaviors (schooling in fishes, flocks of birds) not inherent in individuals. Like other ecosystems, cities are not the sum of their constituents; they are key examples of emergent phenomena, in which each component contributes to but does not control the form and behavior of the whole. Traffic congestion, air pollution, and urban sprawl emerge from local-scale interactions among variables such as topography, transportation infrastructure, individual mobility patterns, real estate markets, and social preferences. What makes urban regions different from many other ecosystems is that in these regions humans are a dominant component.

Cities evolve as the outcome of myriad interactions between the individual choices and actions of many human agents (e.g., households, businesses, developers, and governments) and biophysical agents such as local geomorphology, climate, and natural disturbance regimes. These choices produce different patterns of development (figure 2), land use (figure 3), and infrastructure density (figure 4). They affect ecosystem processes both directly (in and near the city) and remotely through land conversion, use of resources, and generation of emissions and waste. Those changes, in turn, affect human health and well-being (Alberti and Waddell 2000). We propose that *resilience* in cities—the degree to which cities tolerate alteration before reorganizing around a new set of structures and processes (Holling 2001)—depends on the cities' ability to simultaneously maintain ecosystem and human functions.

Cities as complex ecological entities. A diverse literature has begun to document some ecological characteristics of urban regions both in the United States (McDonnell and Pickett 1993, Grimm et al. 2000) and in Europe (Sukopp and Werner 1982, Sukopp et al. 1995). Human-dominated landscapes have unique biophysical characteristics. Humans redistribute organisms and the fluxes of energy and materials. The effects are both obvious (e.g., pavement) and subtle (e.g., conversion of forest to agriculture and then to suburbs; acid rain), both immediate (e.g., dams drown river valleys) and long-term (e.g., new intercity highways direct and promote city growth on 20- to 100-year scales). Relative to non–human-dominated systems, urban ecosystems have low stability, different

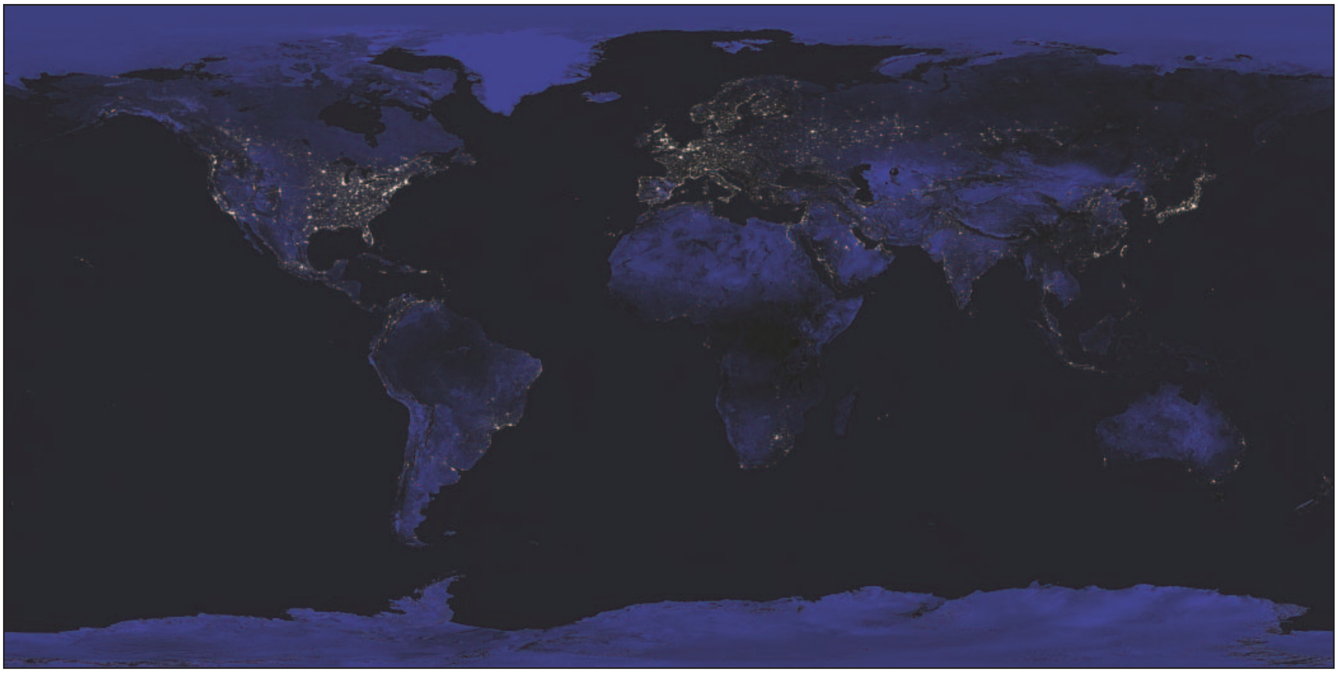

Figure 1. The extraordinary impact of urbanization on Earth is now detectable from space. This composite of satellite images shows how Earth looks at night. Source: National Aeronautics and Space Administration.

dynamics (complex and highly variable on all temporal and spatial scales), more nonnative species, different species composition (often simplified, always changed), and unique energetics (antientropic in the extreme). They have rich spatial and temporal heterogeneity—a complex mosaic of biological and physical patches in a matrix of infrastructure, human organizations, and social institutions (Machlis et al. 1997).

Human activities directly affect land cover, which controls biotic diversity, primary productivity, soil quality, runoff, and pollution. Urbanized areas also modify microclimates and air quality by altering the nature of the land surface and generating heat (Oke 1987). Urbanization's increase in impervious surface area affects both geomorphological and hydrological processes; it changes fluxes of water, nutrients, and sediment (Leopold 1968, Arnold and Gibbons 1996). Because ecological processes are tightly interrelated with the landscape, the mosaic of elements resulting from urbanization has important implications for ecosystem dynamics. The transformation of land cover favors organisms that are more capable of rapid colonization, better adapted to the new conditions, and more tolerant of people than are many endemic, sensitive, locally specialized organisms. As a result, urbanizing areas often have novel combinations of organisms living in unique communities. Mixes of native and nonnative species interact in complex, anthropogenically driven successions, but with human participation, they also equilibrate into communities stable over time. Diversity may peak at

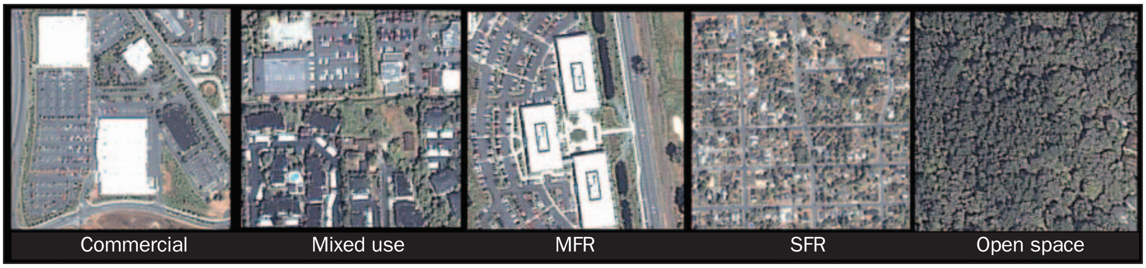

Figure 2. Urban ecological studies need to explicitly represent the complex urban landscape patterns if they are to answer questions about strategies for achieving more sustainable urban forms. Urban development is characterized by different land-use types (industrial, commercial, mixed use, single-family residential [SFR], multifamily residential [MFR], and open space), which exhibit different land-cover composition and configuration. The Urban Ecology Team at the University of Washington is conducting a study that aims to shed some light on the impact of urban patterns on bird diversity and aquatic macroinvertebrates. Data source: IKONOS 2000.

intermediate levels of urbanization, at which many native and nonnative species thrive, but it typically declines as urbanization intensifies (Blair 1996). Rearranging the pattern of land cover also changes the composition of communities; edge species, or those inhabiting interfaces among vegetation types and ecotones (such as white-tailed deer), typically increase, and interior species, or those rarely occurring within a few hundred meters of interfaces (such as northern spotted owls), decline (Marzluff 2001).

Cities as global ecological forcing functions. The importance of cities as drivers of economic development has been recognized for a long time (Jacobs 1961), but their role as a global ecological driving force is not yet fully appreciated (Rees 1992). Many ecological changes forced by cities on their immediate environments are obvious and extreme and have been extensively documented (McDonnell and Picket 1993). Although ecological impacts of urban development often seem to be local, urbanization also causes environmental changes at larger scales. Today's cities are sustained by a socioeconomic infrastructure that operates on global scales; the ecologically productive area required to support an urban area can be 100 to 300 times larger than the urban region (Rees and Wackernagel 1994). Scholars have drawn on the concept of carrying capacity to propose ways to measure a city's ecological footprint (Rees 1992, Rees and Wackernagel 1994) and appropriated ecosystem area (Folke et al. 1996). Rees and Wackernagel (1994) estimate the ecological footprint of Vancouver (British Columbia, Canada) at more than 200 times its geographic area; likewise, Folke and colleagues (1996) estimate that the appropriated ecosystem area required to supply renewable resources to 29 major cities in the Baltic Sea drainage basin is 200 times the total area of the cities.

The spatial organization of a city and its infrastructure affect the resources needed to support the city's human activities and thus the city's level of environmental pressure on the regional and global environment (Alberti and Susskind 1997). The land development needed to house the same number of people varies, depending on choices about location, density, and infrastructure. Whether an urban dweller chooses a private or public transportation system to commute between home and work, for example, depends on the availability of a public transportation system, which in turn depends on the political–economic feasibility of such a system, given the distribution of human activities. These choices have important ecological consequences globally and locally.

Challenges for ecology

The greatest challenge for ecology in the coming decades is to fully and productively integrate the complexity and global scale of human activity into ecological research. How can ecological scholars best study the complex biotic and abiotic interactions within human-dominated ecosystems, the emergent ecology of these systems, and their ecological forcing func-

Figure 3. Development patterns exhibit different degrees of residential density. Data source: IKONOS 2000.

tions? We challenge the assumption that a "human-free" ecosystem paradigm can be productively applied to human-dominated ecosystems. We argue that leaving humans out of the ecological equation leads to inadequate explanations of ecosystem processes on an increasingly human-dominated Earth.

Integrating humans into ecosystems will provide important opportunities for ecosystem science. Consider, for example, how the key ecological concept of the niche could benefit from explicit inclusion of humans. Hutchinson (1957) transformed and solidified the niche concept, changing it from a mere description of an organism's functional place in nature (Elton 1927) to a mathematically rigorous *n*-dimensional hypervolume that could be treated analytically (figure 5). He also emphasized a single dimension of the hypervolume, interspecific competition. Hutchinson's "realized niche" included only those places where an organism's physiological tolerances were not exceeded (its "fundamental" niche) and where its occurrence was not preempted by competitors (figure 5). Emphasizing competition in the niche concept distracted ecologists from investigating other potentially important community organizing forces, such as predation, resources variability, and human domination. A more complete understanding of ecological community assembly has begun to develop (Weiher and Keddy 1999), but it still lacks the inclusion of humans. We suggest that niche theory should distinguish realized from fundamental niches on the basis of human interaction (figure 5). Redefining the realized niche as an organism's hypervolume of occurrence in the presence of a gradient of human domination (figure 5) would quantify the myriad ways humans force population-level ecological functions that structure communities. Understanding the mechanisms of niche assembly in the presence of humans would allow ecologists to directly test the effects of competitors, predators, disease, and land-cover change on community organization, because these ecological processes are often manipulated by humans. The challenge for ecology is to define how humans differ in their effects on ecological processes and, through comparing these differences, to gain clearer insight into how nature works.

An integrated consideration of human interactions with food web complexity may shed light on another ecological contentious ecological principle: the influence of biological diversity on ecological stability. Human domination can increase food web complexity (e.g., by interspersing built and natural habitats; Blair 1996), but this does not necessarily increase ecological or anthropogenic stability (i.e., resilience). Uncoupling the connection between diversity and stability in human-dominated ecosystems highlights the importance of species identity, rather than simply species richness, to community stability. Investigating the changing relationship between diversity and stability along a gradient of human domination can clarify when diversity begets stability, when diversity simply means unnecessary redundancy of ecological roles, and when diversity leads to instability (e.g., diversity resulting from importation of invasive exotics).

Figure 4. Differing infrastructure densities imply varying degrees of land-cover change and fragmentation in urbanizing areas. Data source: IKONOS 2000.

Traditional ecological investigations of populations and communities could benefit from studying human-dominated ecosystems, as we suggest above. This has been shown, for example, by studies of the dynamics of nutrient cycling and energy flow that have begun to incorporate human domination (Vitousek et al. 1986, 1997a). These studies have enabled better prediction of ecosystem-level processes and have led to a greater appreciation of human influences on the planet.

A conceptual model for urban ecology

Ecologists are paying increasing attention to the relationship between urbanization and ecosystems (Collins et al. 2000, Grimm et al. 2000, Pickett et al. 2001), but few have directly addressed how human and ecological patterns emerge from the interactions between socioeconomic and biophysical processes. Current study of urban ecosystems uses such simplified representations of human–ecological interactions that their system dynamics cannot be fully appreciated and understood. For example, most ecological studies treat urban areas as homogeneous phenomena and combine all anthropogenic factors into one aggregated variable (e.g., pollution load, population density, total paved area); thus, they represent urbanization as unidimensional. This is unrealistic: Urbanization is multidimensional and highly variable across time and space. Socioeconomic studies, on the other hand, highly simplify and rarely discriminate among different and complex ecological and biophysical processes. This aggregate representation of human and ecological processes

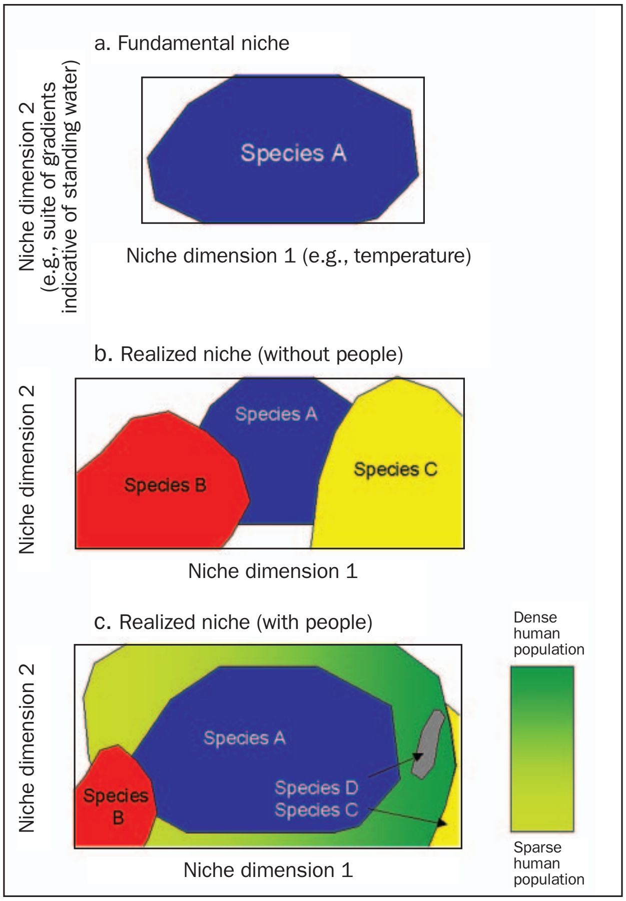

Figure 5. The fundamental niche of a species (those areas on Earth where its physiological tolerance limits are not exceeded) is an n*-dimensional hypervolume, where each environmental gradient relevant to a species is one dimension (Hutchinson 1957). (a) A two-dimensional view of two axes from the* n*-dimensional Hutchinsonian niche hypervolume for species A, which can exist in areas with moderate temperature and moderate relative humidity. We contend that theoretical ecologists have steered empiricists away from fully understanding how communities are assembled by emphasizing competition in the formalization of the niche concept. A better paradigm for understanding how biotic communities are structured is to document the effect of humans on species' realized niches. (b) The Hutchinsonian realized niche is that portion of the fundamental niche not preempted by competitors, shown here for three species in the absence of people. (c) In this model of a realized niche with human involvement, Species A (e.g., a human commensal, such as the Norway rat) expands to fill its fundamental niche in the presence of people. Species B has a restricted distribution because the human-subsidized species A outcompetes it. Species C is intolerant of humans and is confined to portions of its fundamental niche where people do not exist. Species D is imported by humans into the geographic niche space indicated in (c). As humans dominate more of Earth, the types of processes that assembled and structured this community (niche space) are fast becoming the rule rather than exception.*

cannot explain human–environment interactions in human-dominated systems, nor can it allow ecological scholars to fully understand the complex dynamics of such systems, because many of these interactions occur at levels not represented in current integrated approaches (Pickett et al. 1994).

Ecologists and social scientists have studied emergent ecological and social phenomena, but they have not explored the landscape-level implications of interactions between social and ecological agents. In their separate domains, neither the natural nor the social sciences can explain how integrated human and ecological systems emerge and evolve, because human and ecological factors work simultaneously at various levels. Ecologists have studied self-organized patterns in social insect colonies composed of hundreds to millions of genetically similar individuals. These individuals interact locally, but collectively they produce large-scale colony dynamics that are not predictable from the individuals' characteristics. Urban planners, economists, and sociologists have described cities as self-organizing systems in which emergent bottom-up processes create distinct neighborhoods and unplanned demographic, socioeconomic, and physical clusters. The need to share local services and a customer base drives residents and businesses together, while competition for land, labor, and customers drives them apart. Because of these forces, initial random distributions in human-dominated landscapes rearrange spontaneously into a self-organized pattern with multiple diverse clusters (Krugman 1995).

To fully integrate humans into ecosystem science, we propose a new conceptual model that links human and biophysical drivers, patterns, processes, and effects (figure 6). Although several new models address the relationship between urbanization and ecosystem dynamics (Collins et al. 2000, Grimm et al. 2000, Pickett et al. 2001), they do not explicitly represent the interactions between human and biophysical patterns and processes, nor do they represent the feedbacks from these interactions. In our model, both biophysical and human agents drive the urban socioeconomic and biophysical patterns and processes that control ecosystem functions. Using this framework, ecological scholars can ask questions about how patterns of human and ecological responses emerge from the interactions between human and biophysical processes and how these patterns affect ecological resilience in urban ecosystems. This model can help test formal hypotheses about how human and ecological processes interact over time and space. It can also help establish (a) what forces drive patterns of urban development, (b) what the emerging patterns are for natural and developed land, (c) how these patterns influence ecosystem function and human behavior, and (d) how ecosystem and human processes operate as feedback mechanisms. Without a fully integrated framework, scholars can neither test hypotheses about the systems' dynamics nor produce reliable predictions of ecosystem change under different human and ecological disturbance scenarios. Such knowledge is critical if managers and policymakers are to control and minimize the effects of human activities on ecosystems.

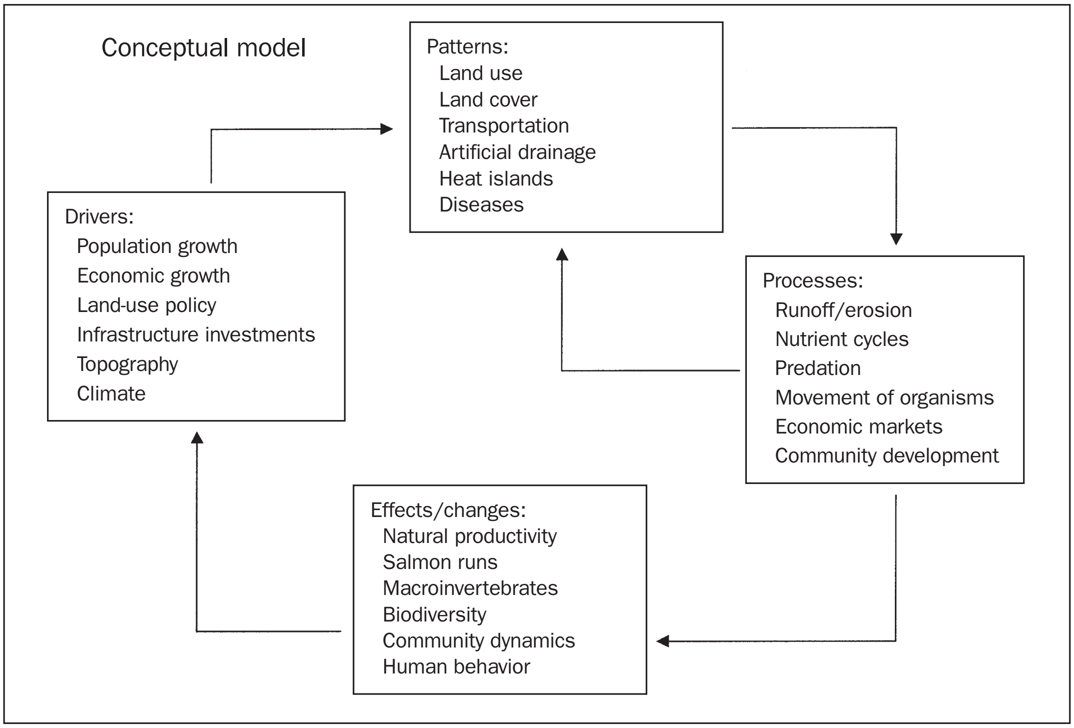

Figure 6. An integrated model of humans and ecological processes to understand forces driving patterns of urban development, quantify resulting patterns of natural and developed land, determine how these patterns influence biophysical and human processes, and assess the resulting environmental changes and feedback on human and biophysical drivers. In this conceptual model, drivers are human and biophysical forces that produce change in human and biophysical patterns and processes. Patterns are spatial and temporal distributions of human or biophysical variables. Processes are the mechanisms by which human and biophysical variables interact and affect ecological conditions. Effects are the changes in human and ecological conditions that result from such interactions. In the diagram we provide some explicit examples of drivers, patterns, processes, and effects. For example, population growth in an area (driver) leads to increased pavement and buildings (patterns), leading to increased runoff and erosion (processes), causing lower water quality and decreased fish habitat (effects), which may lead to a new policy to regulate land use (driver). However, the same variable can fit into different boxes depending on the focus (issue, scale, and time frame). For example, erosion is a process, but it can also be seen as a pattern that influences other processes such as nutrient cycles or as an effect resulting from runoff.

An example: Urban sprawl

Urban sprawl illustrates the complexity of interactions and feedback mechanisms between human decisions and ecological processes in urban ecosystems. Sprawl manifests as a rapid development of scattered (fragmented), low-density, built-up areas ("leapfrogging"; Ewing 1994). Between 1950 and 1990, US metropolitan areas grew from 538,720 square kilometers (km^2) (84 million people) to 1,515,150 km^2 (193 million people). Land development due to urbanization has grown 50% faster than population (Rusk 1999). Sprawl is driven by demographics (e.g., increases in numbers of households), socioeconomic trends (e.g., housing preferences, industrial restructuring), and biophysical factors (e.g., geomorphological patterns and processes) and is reinforced by infrastructure investment choices (e.g., development of highway systems; Ewing 1994). Sprawl is strongly encouraged by land and real estate markets (Ottensmann 1977) and is now a highly preferred urban living arrangement (Audirac et al. 1990).

The phenomenon of sprawl shows how considering only aggregated interactions between humans and ecological processes cannot help explain some important mechanisms that drive human-dominated ecosystems. Human decisions are the primary driving force behind environmental conditions in urban ecosystems, but these conditions cannot be explained by taking separately the behavior of individual agents (e.g., households, businesses, developers) competing in each market (e.g., job market, land and real estate market). Households, which are themselves complex entities, simultaneously compete in the job and real estate markets when deciding where to live. Furthermore, these agents have preferences and make tradeoffs that are highly dependent on biophysical factors. Decisions about land development and infrastructure are strongly influenced by biophysical constraints (e.g., topography) and environmental amenities (e.g., "natural" habitats). From local interactions among these agents eventually emerge metropolitan patterns, which in turn affect both human and biophysical processes. Resulting changes in environmental conditions then strongly influence some important human decisions. Furthermore, in these systems, uncertainty is important, since any departure from past trends can affect system evolution.

Sprawl has important economic, social, and environmental costs (Burchell et al. 2002). It fragments forests, removes native vegetation, degrades water quality, lowers fish populations, and demands high mobility and an intensive transportation infrastructure. Such environmental changes may eventually make suburban sprawl areas less desirable for people and may trigger more development at increasingly remote locations. But urban feedback is changed in form and is phase-lagged, often by decades (e.g., results of decisions on highway development). Municipalities are largely responsible for promoting sprawl. For example, cities often subsidize sprawl by providing public services (schools, waste disposal, utilities) that are priced independent of their real cost and distance from central facilities (Ewing 1997), so that residents in the sprawled periphery usually do not pay the full costs of their own services (Ottensmann 1977).

The "complex system" paradigm provides a powerful approach for studying urban sprawl as an emergent phenomenon and for devising effective policies to control its effects. Complex structures can evolve from multiple agents operating according to simple decision rules (Resnick 1994, Nicolis and Prigogine 1989). Some fundamental attributes of complex human and ecological adaptive systems—multiple interacting agents, emergent structures, decentralized control, and adapting behavior—can help scholars to understand how urbanizing landscapes work and to study urban sprawl as an integrated human–ecological phenomenon. Complex metropolitan systems cannot be managed by a single set of top-down governmental policies (Innes and Booher 1999); instead, they require the coordinated action of multiple independent players operating under locally diverse biophysical conditions and constraints, constantly adjusting their behavior to maintain an optimal balance between human and ecological functions.

A research agenda for urban ecology

We believe that a radical change is needed in how scholars frame questions about urban ecology. Instead of "How do socioeconomic phenomena affect ecological phenomena?" the question should be "How do humans interacting with their biophysical environment generate emergent collective behaviors (of humans, other species, and the systems themselves) in urbanizing landscapes?" Theories about complex adaptive systems provide tools with which to analyze how landscape-scale organization of structures and processes arises in urbanizing regions; how it is maintained; and how it evolves by local interactions of processes that occur at smaller scales among social, economic, ecological, and physical agents (self-organization). These theories also provide a new framework for understanding how distributed control, information processes, and adaptation in human-dominated systems should guide the development of policies to effectively balance human and ecosystem functions in urbanizing regions. Specifically, urban ecology scholars need to address four fundamental questions:

1. How do socioeconomic and biophysical variables influence the spatial and temporal distributions of human activities in human-dominated ecosystems?
2. How do the spatial and temporal distributions of human activities redistribute energy and material fluxes and modify disturbance regimes?
3. How do human populations and activities interact with processes at the levels of the individual (birth, death, dispersal), the population (speciation, extinction, cultural or genetic adaptation), and the community (competition, predation, mutualism, parasitism) to determine the resilience of human-dominated systems?
4. How do humans respond to changes in ecological conditions, and how do these responses vary regionally and culturally?

Our conceptual framework provides a new theoretical basis to test formal hypotheses about the mechanisms that link urban patterns and ecosystem dynamics at multiple scales and about the influence of these mechanisms on the resilience of urban ecosystems. First, we hypothesize that both biophysical and human agents drive the urban socioeconomic and biophysical patterns and processes that control ecosystem functions. Second, we hypothesize that patterns of development (urban form, spatial organization of land use, and connectivity) influence ecosystem dynamics. Third, since alternative patterns of urbanization affect the ability of a system to maintain a balance between human and ecosystem services, we hypothesize that the patterns generate differential effects on ecological resilience. Fourth, we hypothesize that in complex human-dominated ecosystems, changes at one level of the biological and social organization can alter emergent human–ecological phenomena at another level.

Driver hypotheses. Urban ecosystems provide an excellent gradient to test hypotheses on emergent human–ecological phenomena. A complex set of social, political, economic, and biophysical factors drives urbanization and affects when, where, how, and at what rate urban development proceeds. In studying interactions between human and ecological processes, researchers need to address explicitly the complexities of many factors working simultaneously on scales from the individual to the regional and global. Consideration solely of aggregated interactions cannot help explain or predict important feedbacks or outcomes, so testable models must be spatially referenced ever more explicitly and finely. Lag times between human decisions and their environmental effects further complicate understanding of these interactions. For instance, in urban ecosystems, land-use decisions affect species composition directly (e.g., introduction and removal of species) and indirectly (e.g., modification of "natural" disturbance agents like fire and flood). If ecological productivity controls the regional economy, interactions between local decisions and local-scale ecological processes can cause large-scale environmental changes (Alberti 1999).

Pattern hypotheses. A second set of hypotheses that can be effectively tested in urbanizing landscapes concerns the effects of human–ecological patterns on human and ecological processes. Landscape ecologists and urban planners debate relationships between spatial patterns of urban development and ecological conditions, but few empirical studies have provided evidence of mechanisms linking urban patterns to ecological and human functions in urbanizing landscapes. We argue that different urban patterns (i.e., urban form, land-use distribution, and connectivity) generate differential effects on ecosystem dynamics and therefore differ in their ecological resilience. This is because urban development patterns differently affect the amount and interspersion of built and natural land cover as well as anthropogenic demands on ecosystem services. We hypothesize that ecological and socioeconomic conditions can be discriminated across a gradient of urbanization patterns.

Resilience hypothesis. We hypothesize that resilience in an urban ecosystem depends on multiple human and ecological services provided by natural and human systems. To assess that resilience, researchers must understand how interactions between humans and ecological processes affect the inherently unstable equilibria between the end points of the urban gradient. Over the long term, human services in urban areas (housing, water supply, transportation, waste disposal, recreation) all depend on ecosystem functions for their productivity (Costanza et al. 1997, Daily 1997). Integrating humans into ecology will help identify the thresholds to best balance human and ecosystem services in urban ecosystems.

Scale hypotheses. One critical problem in urban ecology is understanding how change at one level of biological and social organization will alter emergent patterns or mechanisms at another level. A hierarchical approach has been proposed to better explore the relationship between top-down and bottom-up forces in determining ecosystem dynamics (Wu and David 2002). Urban ecosystems provide the best setting to test hypotheses on the dynamic hierarchical structure of human-dominated landscapes. Such knowledge would make it easier to manage complex, human-dominated ecosystems successfully. For example, in working to maintain biodiversity, managers usually begin at the species level, but this misses the fundamental importance of biodiversity at other scales: Higher-level biodiversity provides interconnections between multiple elements operating at multiple levels and transforms the community from a random collection of species into an ecosystem of interrelated biotic and abiotic parts (Levin 1998).

Practicing a new urban ecology

Effective integration of humans into ecological theory, which is both beneficial and necessary in order to better understand ecological systems in general, and human-dominated systems in particular, requires effective team building, interdisciplinary training, and a new dialogue between science and policymaking.

Effective team building and education. Most of today's scientific and social problems lie at the interface of many scientific disciplines. Strategic decisions about how best to address urban growth require the synthesis of extraordinarily complex and rapidly evolving knowledge from a broad range of disciplines (e.g., forestry, fisheries, urban planning, zoology, civil engineering, landscape architecture, geography, political science, sociology, psychology, and economics). Effective approaches require high-performance teamwork. It is naive to assume that scholars trained in a single discipline can successfully create interdisciplinary research teams and teach in interdisciplinary settings. To effectively bridge gaps among disciplines, scientists need to learn new skills with which to frame problems and design solutions that address multiple perspectives simultaneously. To achieve this level of synthesis, scientists need to be aware of their own mental models, disciplinary biases, and group dynamics. This requires (a) investigating differences between disciplines (what the values are; how questions are posed; what constitute valid data; how data are gathered, processed, and reasoned about) and (b) understanding and managing group dynamics.

This awareness comes slowly to established scientists, but it can evolve rapidly if the next generation of urban ecologists is trained in a new way. Our experience suggests that students of urban ecology need strong disciplinary bases, but they especially need qualities rarely developed by traditional graduate programs: interdisciplinary experience, breadth, flexibility, team building, and sophisticated skills in communication and synthesis. These skills can be layered on strong disciplinary foundations by graduate education that emphasizes interdisciplinary and team-based research focused on real-world problems. Students must understand the differences in how social scientists, ecologists, managers, and policymakers formulate and define problems, ask questions, gather and evaluate information, and propose and implement solutions. Students who receive such training will improve relationships among academic, business, regulatory, and urban communities.

A new relationship between science and policy. Urban ecology ultimately involves studying how to integrate this new interdisciplinary knowledge about urban ecosystems into policymaking processes—to improve interactions between policymakers and scientists so as to help society achieve more sustainable urban forms. Today, the scientific and political communities lack the effective two-way communication and trust that they need to address urban ecological problems. A number of factors contribute to this division between science and policy. Society sets goals through the policy process, which is not solely driven by science's commitment to analytical norms and searching for "truth." Although science can help society formulate a range of options to achieve societal goals, it cannot make value judgments. In addition, scientists often cannot deliver definitive answers to questions posed by policymakers. Scientists often disagree about causes of environmental problems, so policymakers need to act under scientific uncertainty. Policymakers often claim they cannot afford to wait for "scientifically correct" answers to problems. Furthermore, even when causal knowledge exists on environmental problems, it does not necessarily lead to action. The urban ecology's scientific community needs to participate actively to inform policymaking and make scientific results relevant to policy decisions, even though most scientists receive little training on the policy process. In the same way, policymakers must participate in formulating scientific questions and defining priorities if science is to become relevant in decisionmaking. Inviting policymakers into the classroom to help shape graduate research projects helps forge this new relationship.

Toward consilience? Urban ecology holds great promise for advancing ecological understanding, providing society with important information that can encourage sustainable development, and allowing social and biological scientists to effectively integrate information. Together, these objectives may lead toward the consilience, or unity of knowledge across fields, that Wilson (1998) argues has eluded science. This unity of sciences and humanities must become the backbone of urban ecology. Without it, socially relevant and ecologically accurate research will not materialize, policy decisions will be made without the full benefit of relevant scientific information, and cities will continue to grow in increasingly unsustainable ways. Employing a unified approach, the next generation of urban ecology scholars can conduct interdisciplinary research, and practitioners can provide society with the tools to set and prioritize goals, make informed tradeoffs, and develop and implement policies toward more sustainable urban development.

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