A New Urban Ecology

Modeling human communities as integral parts of ecosystems poses special problems for the development and testing of ecological theory

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The science of ecology was born from the expansive curiosity of the biologists of the late 19th century, who wished to understand the distribution, abundance and interactions of the earth's organisms. Why do we have so many species, and why not more, they asked—and what causes them to be distributed as they are? What are the characteristics of a biological community that cause it to recover in a particular way after a disturbance?

Such questions took Charles Darwin and other naturalists on journeys far from human civilization. And more than a century later, ecologists still tend to search for answers to these questions in "pristine" environments—the tropical rain forest, the coral reef. From the perspective of a field ecologist examining a natural ecosystem, people are an exogenous, perturbing force. Human beings—and especially their cities, seemingly so "artificial"—fail to fit neatly into ecological theory.

But people mobilize nutrients and pollutants, drive species extinct, promote the survival of others, change the composition of the atmosphere and alter landscapes. Thanks to advances in technology and to humanity's growing population and penchant for consumption, we are today a global ecological force capable of affecting every species and ecosystem on the planet. Over the past several decades, moreover, we have rushed to the cities. Soon more people worldwide will live in cities than in rural areas. In cities people mobilize some nutrients and deplete others, create habitats that never before existed, divert water, increase temperatures and, by intent or by accident, manipulate the communities of other species found within city boundaries and beyond. Cities are some of the most profoundly altered ecosystems on the planet; within their boundaries are also found some of the most diverse ecological conditions. If there is a laboratory where ecological change can be viewed at close hand, it is the city.

Ecologists, however, have hardly rushed to the city. A mere 0.4 percent—25 of 6,157—of the papers published in nine leading ecological journals in the past five years dealt with cities or urban species. Whatever the reasons for ecologists' persistent tendency to focus on pristine environments, human-dominated ecosystems represent a problem for the field. We lack a method of modeling ecosystems that effectively incorporates human activity and behavior. And the processes and dynamics within cities largely elude an understanding based on traditional ecological theories.

Yet an increasing number of ecologists are calling for a change in focus, and there are indications that this change is under way. The National Science Foundation recently extended its network of Long-Term Ecological Research (LTER) sites to two urban environments—Baltimore and Phoenix. We are enthusiastic participants in this work, and we believe that there is no better place than the city to develop hypotheses and test predictions that emerge when one attempts to adapt ecological theory to include humans.

In this article we attempt to define the modeling issues facing this new type of "urban ecology," which will strive to understand people and their urban behavior in the inclusive way the first ecologists tried to understand remote tropical isles—defining and studying the interactions between people and the so-called natural environment in which their cities exist. In our view ecosystems span a continuum, from the pristine to the urban, along which the role of human activity grows from marginal to dominant. It is interesting that the term "urban ecology" was coined by sociologists who sought to use ecological theory to describe human behavior in the urban setting. Today we are attempting to integrate human-dominated ecosystems into ecology itself.

Essentially we wish to present a challenge to classical ecological theory: If orthodox theory is truly general, then it should be able to explain the distribution, abundance and relationships of organisms and their environments—including human beings and associated species in urban environments. If orthodox theory cannot be generalized to encompass human-dominated environments, then ecologists will need to revise it. Scientists are key participants in the struggle to maintain the world's biodiversity and

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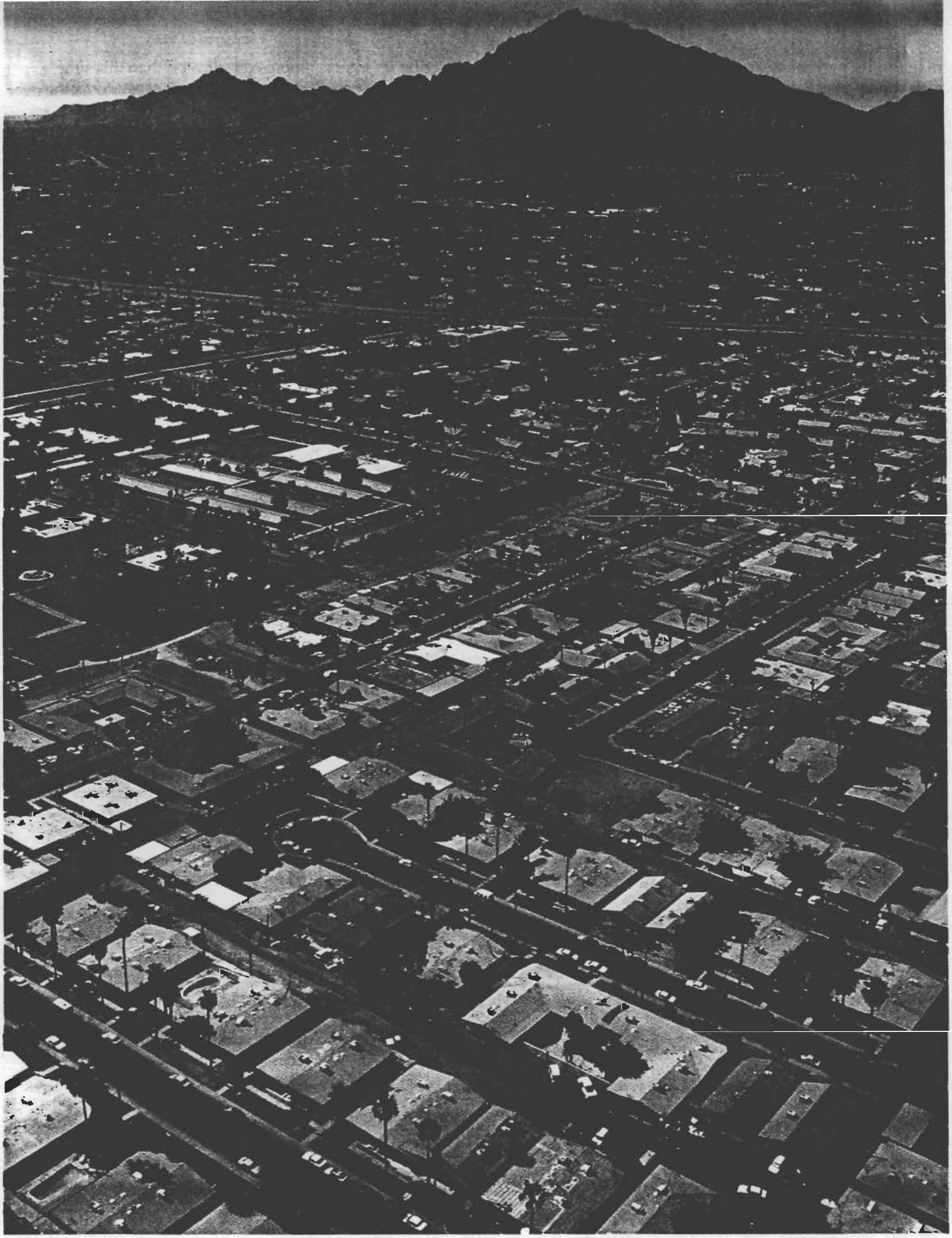


Figure 1. Fast-growing Phoenix forms a sprawling island in the Arizona desert, a visual reminder that every ecological parameter, from the pattern of environmental disturbance to the scale of competition among species, is affected by human activity. Historically ecologists have tested their theories in "pristine" environments, but attention is turning at last to the urban ecosystem, which does not easily conform to existing ecological theory. The authors argue for an integration of urban and traditional ecology and the incorporation of social-science models into the scientific view of how human activity affects other organisms and alters ecosystem structure and function. (Photograph by Corinna Gries, Arizona State University.)

manage its natural resources. Ecologists cannot effectively contribute without models that incorporate the activities of our own species.

A Dependent Ecosystem

Urban-ecology research at this stage consists of vastly more questions than answers. If ecologists are to study urban ecosystems, for instance, they must decide two questions first: what an urban ecosystem is, and what measures appropriately describe its interactions with other ecosystems? In some respects these are the same question—and a good place to begin.

Among the traditional ways to look at an ecosystem is by examining how it balances primary production (photosynthesis, or solar-energy conversion by plants) with respiration, by which energy is converted to unusable form. Although the calculations that make up a system's internal energy budget are far more complicated than this simple ratio suggests, for most ecosystems the overall calculation is fairly well balanced between inputs and outputs. An urban ecosystem, a concentration of people and human activity, is an energy-intensive ecosystem, and viewed in traditional ecological terms it is more unbalanced than most other ecosystems. Its unique energy signature, then, is one way of distinguishing an urban ecosystem.

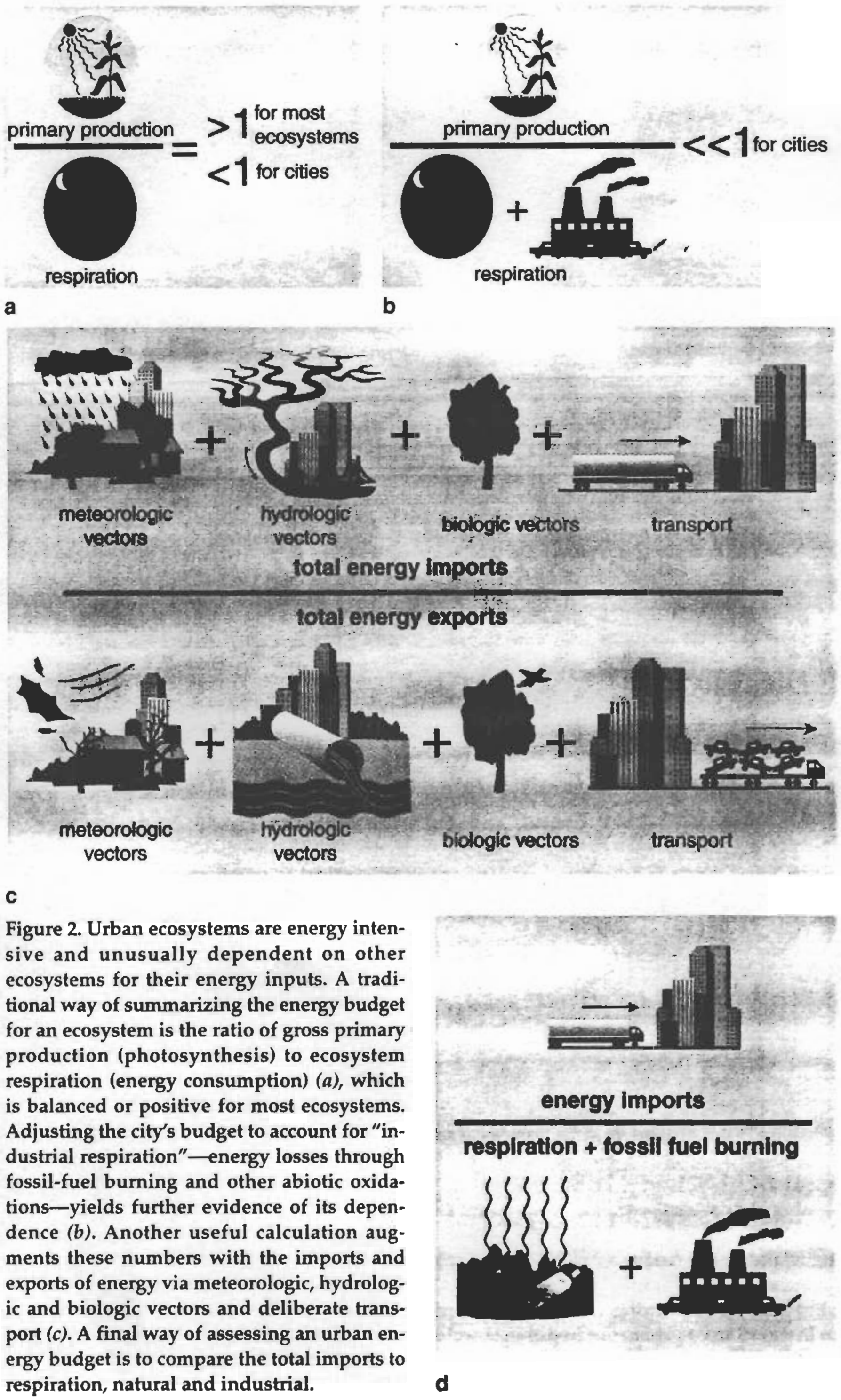


Figure 2. Urban ecosystems are energy intensive and unusually dependent on other ecosystems for their energy inputs. A traditional way of summarizing the energy budget for an ecosystem is the ratio of gross primary production (photosynthesis) to ecosystem respiration (energy consumption) *(a)*, which is balanced or positive for most ecosystems. Adjusting the city's budget to account for "industrial respiration"—energy losses through fossil-fuel burning and other abiotic oxidations—yields further evidence of its dependence *(b)*. Another useful calculation augments these numbers with the imports and exports of energy via meteorologic, hydrologic and biologic vectors and deliberate transport *(c)*. A final way of assessing an urban energy budget is to compare the total imports to respiration, natural and industrial.

Howard T. Odum of the University of Florida noted that a typical city daily transforms into heat about 70 times more usable energy per square meter than a close nonhuman equivalent to a city—an oyster reef. A natural ecosystem is likely to be self-powered by photosynthesis or chemosynthesis. By contrast a city is a *heterotrophic* ecosystem, one that depends primarily on external sources of energy. Take Chicago's famed pizza: It may be made with wheat from Kansas, tomatoes from California, anchovies from the Mediterranean and cheese from a Wisconsin dairy farm. The pizza oven may be fired with fuel from the Middle East and made of steel forged in Pennsylvania or perhaps Japan. Pizza-making thus borrows, in one form or another, energy that originated with photosynthetic activity in other ecosystems. Heterotrophic ecosystems are rare on earth, including some marshes, the deep ocean and streams, but even among such systems cities are extreme.

There are a variety of ways of describing flows between urban areas and other ecosystems *(Figure 2)*. One is an input-output model. People import to cities foodstuffs, fuels, building materials and other products that can be described in the energy currency of ecology. Land conversion or degradation, agricultural production and the harvesting of plant-derived building materials can be seen as ways in which the urban ecosystem appropriates the primary production of other ecosystems. In addition, we can consider *how* energy flows: Imports and exports are mediated by meteorologic, hydrologic and biologic vectors. A city along a river, for instance, imports energy via hydrologic vectors from an entire watershed and typically returns to the downstream environment water containing heat and nutrients such as phosphorus and nitrogen.

Urban energy budgets, dominated as they are by deliberate human energy imports and by losses via fossil-fuel burning, or "industrial respiration," do

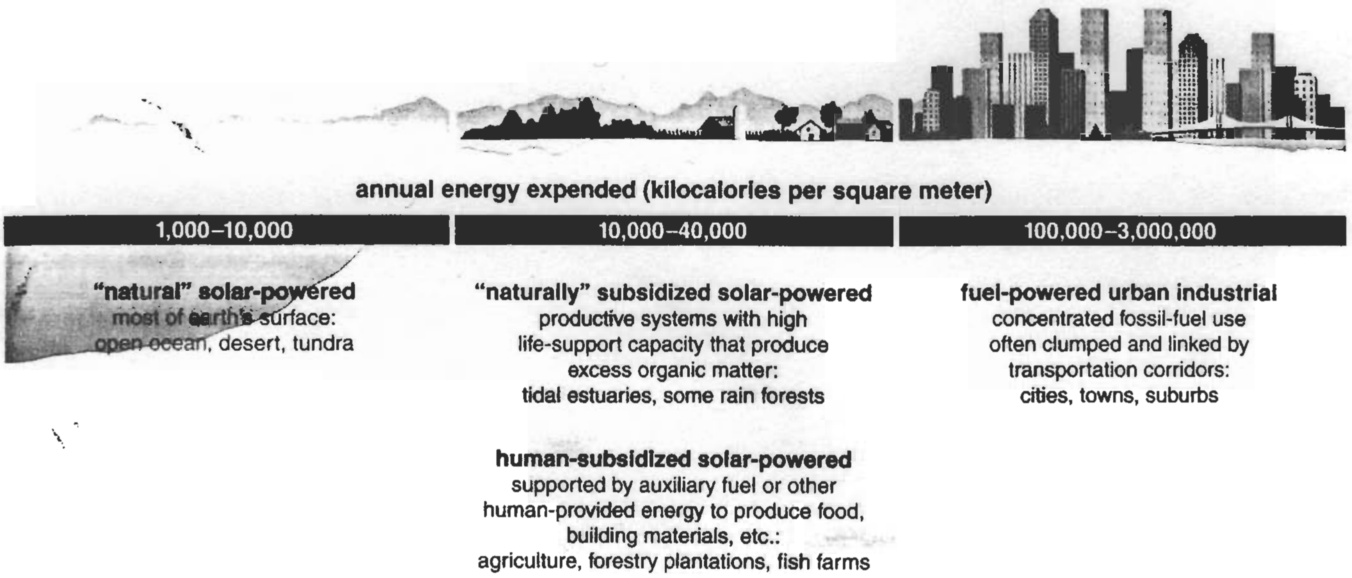


Figure 3. Eugene P. Odum has categorized ecosystems based on their energy intensity. Life on most of the earth's surface derives its energy from solar power without a "subsidy"—an excess productivity or capability of supplying more food than its organisms need. The energy expended in unsubsidized systems *(left side)* is less than 10,000 kilocalories per square meter. Higher energy intensity is found in "subsidized" systems such as coastal upwelling zones. Human-dominated ecosystems are subsidized by auxiliary fuel, and many—farms, tree plantations and residential neighborhoods—are comparable in energy intensity to highly active natural ecosystems. Urban industrial ecosystems are characterized by a concentrated use of fossil fuels and can reach an energy intensity of 3 *million* kilocalories per square meter.

not resemble the energy budgets of any other ecosystem on earth, as the work of Eugene P. Odum of the University of Georgia has shown *(Figure 3)*. Although calculating these budgets can be complex, energy use is a common currency that can be measured for all ecosystems, providing a basis for comparing systems that are human dominated with those that are not. Ecology has been called "nature's economy," and such calculations potentially afford a means for linking ecological theory with social-science theories using resource-economics concepts.

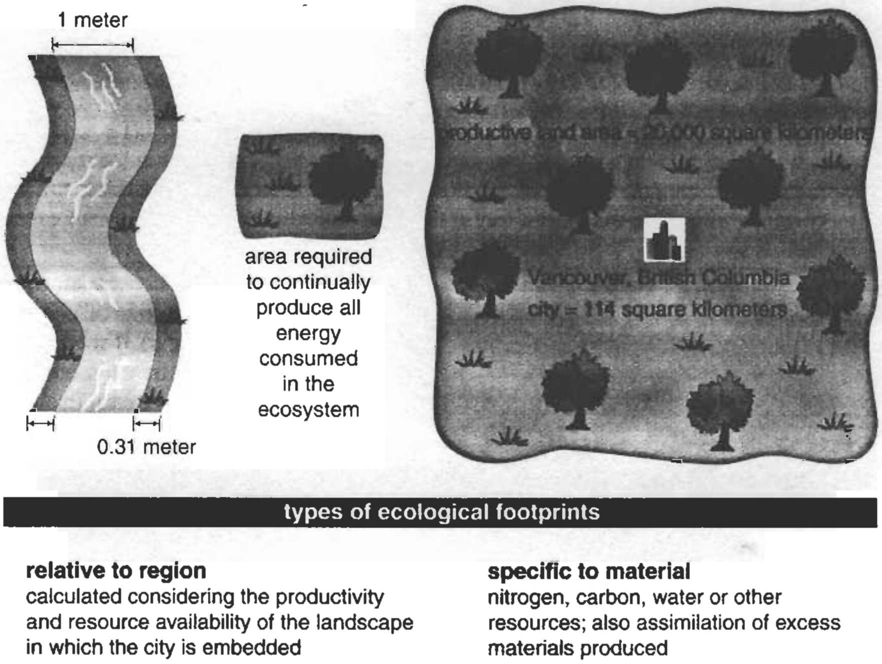


Figure 4. Ecological "footprint" is a novel way of describing an ecosystem's dependence on its surroundings and comparing urban ecosystems to others. Bear Brook, New Hampshire is heterotrophic—sustained by energy supplied from outside. The stream's energy consumption, or respiration, amounts to 2,935 kilocalories per square meter annually. The annual net primary production of the surrounding forest is 4,680 kilocalories per square meter. If organic matter imported from the forest supplied all the stream's energy needs, the forest area needed would be equivalent to a riparian strip measuring 0.31 meter wide on either side of a one-meter-wide stream. By contrast, the city of Vancouver, British Columbia consumes an amount of material equivalent to that produced by 20,000 square kilometers of productive land—180 times the city ecosystem's area. Described are two ways of calculating a footprint. (Data from Fisher and Likens 1973, Rees and Wackernagel 1996.)

The Urban Footprint

The different characteristics of urban ecosystems may call for some nontraditional ways of assessing *how* dependent they are on other ecosystems.

Consider the comparison in Figure 4. Stuart Fisher and Gene Likens, both then at Dartmouth College, working in the Hubbard Brook Experimental Forest of New Hampshire, examined the heterotrophic ecosystem of Bear Brook. Primary production was negligible in the stream itself, and all of the ecosystem's respiration (2,935 kilocalories per square meter annually) was supported by material imported from the surrounding forest, which had an annual net primary production of 4,680 kilocalories per square meter. Yet the amount of material

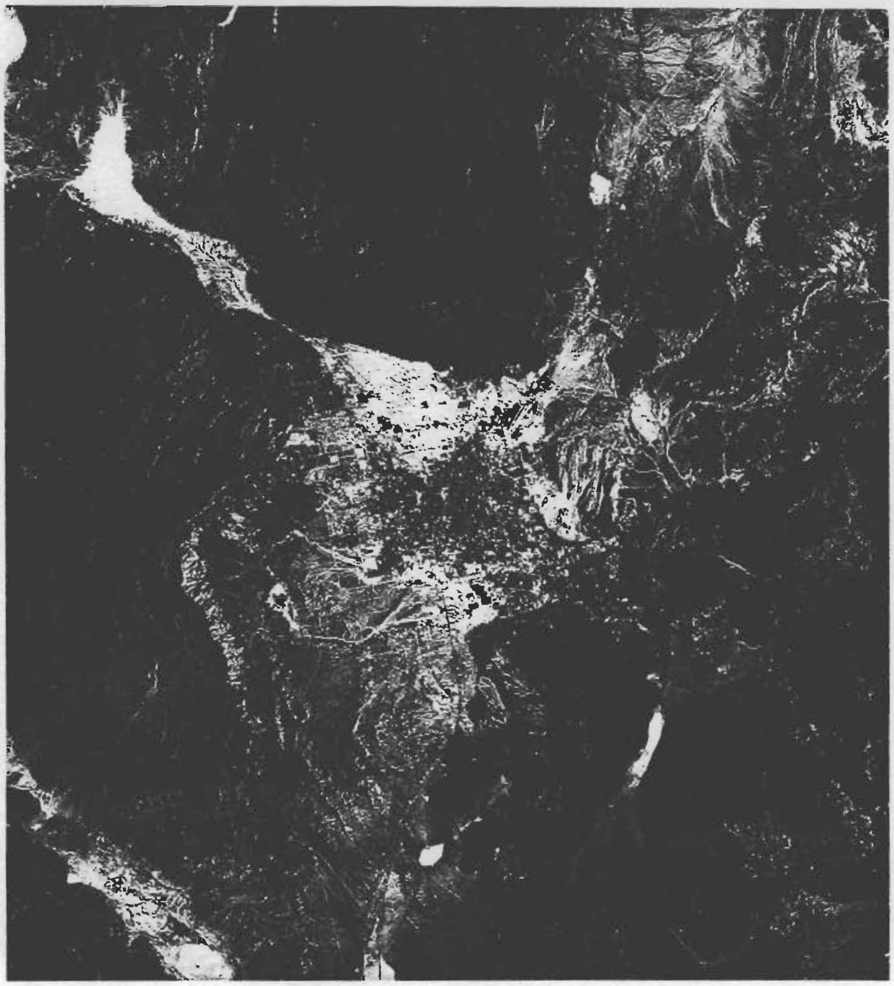


Figure 5. Ecological footprint of a city in an arid environment may be larger in land-area terms because the productivity of desert ecosystems is low. A 1993 Landsat image of Las Vegas, Nevada in its desert environment (Lake Mead is to the right) shows that natural vegetation *(dark red)* is sparse. Most biological productivity is supplied by irrigated agricultural lands and grass *(bright red)* within the urban area, yet this productivity is very small compared with the city's energy consumption. (Image courtesy of the U.S. Geological Survey EROS Data Center.)

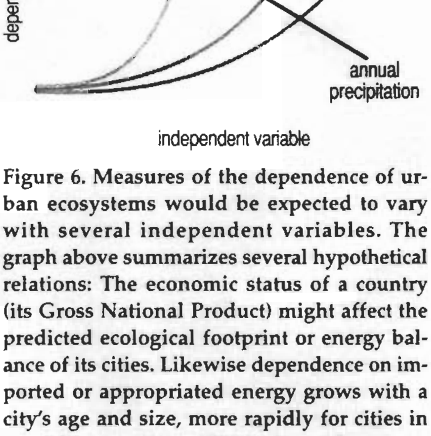


Figure 6. Measures of the dependence of urban ecosystems would be expected to vary with several independent variables. The graph above summarizes several hypothetical relations: The economic status of a country (its Gross National Product) might affect the predicted ecological footprint or energy balance of its cities. Likewise dependence on imported or appropriated energy grows with a city's age and size, more rapidly for cities in wealthier nations. Cities in arid regions should have larger footprints.

required could be supplied by an area of forest equivalent to a strip of vegetation about two feet wide (0.31 meters on each bank) along the stream's length, much narrower than the stream itself.

By contrast, William Rees of the University of British Columbia estimated that the city of Vancouver consumes an amount of material equivalent to that produced by a productive land area 180 times its size, assuming that area is not dominated by people.

Rees employs in his analysis an instructive measure of urban energy dependence called an "ecological footprint." The footprint of a city is the total area of productive land required to support its activities in a sustainable way. In other words, that land must produce an amount of resources equivalent to the sum of all resources consumed by the city—and assimilate an amount of waste equivalent to that produced by the city. Cities' footprints can be impressive—tens or hundreds of times larger than their actual area—because in addition to the plant, microbial and animal metabolisms that characterize all ecosystems, cities have an "industrial metabolism"—a metaphorical hunger whose satisfaction requires mining of nonrenewable resources as well as exploitation of renewable ones.

The footprint concept is a new (and somewhat controversial) way of assessing ecosystem dependence. Matthew Luck and other LTER scientists at ASU are exploring, among other questions, how the concept of a footprint could be used to consider the impact of a city within its particular geology and climate. Many of the earth's fastest-growing cities are, like Phoenix, located in low-productivity arid or semi-arid lands. In terms of land area, these cities' footprints are huge, if this local context is taken into account.

Local conditions are just one of several independent variables that would be expected to influence the magnitude of an urban ecosystem's dependence on its surroundings. Others are the fertility of the surrounding land, the average income of the city's inhabitants, cultural variables, a city's size and age, and its political context. And this general dependence measure could be partitioned into separate measures for different ecological variables such as water, elements, food, waste assimilation and energy.

We can make some predictions of the interaction between footprint and the independent variables based on observation *(Figure 6)*. The footprint will be largest for mature, large cities within affluent nations that lie within arid regions. These are not necessarily linear relations: Large cities and small cities differ in significant ways, and there may be a "leveling off" of the dependence curve as a city in an affluent nation matures. Overall, as a city grows, its footprint would be expected to grow faster if it is located in an affluent region.

The City in Space and Time

Since the characteristics of any ecosystem vary from one part to another, ecologists conceive of ecosystems as consisting of habitat "patches." A city—with its concrete-and-glass downtown, its golf courses, industrial parks and tree-lined residential streets—is quite a patchy ecosystem, and together with all its patches it is part of a larger landscape full of other patches. A landscape ecologist tackling an urban ecosystem would look at the pattern of patches within a city, and the variations in the way the land is used from one patch to the next, and ask how these patterns and this variability influence biogeochemical processes and affect how organisms and resources are distributed, and how species interact.

As the pioneering ecologist C. C. Adams observed early in the 20th century, ecology will need to incorporate the social sciences to answer such questions when human beings are taken into account. Models to explain how people as a species affect the composition of habitat patches and their patterns will have to integrate historical, political, cultural and economic factors with traditional variables such as competition, predation and nutrient availability, which also control the distribution, abundance and relations of organisms.

But we can begin by looking for spatial patterns. Traditionally these include the species composition of patches and how the patches are arranged in space. These variables affect ecological processes by regulating competition among species and energy flows within the ecosystem. The scale of the pattern also affects the scale at which these processes operate. Such patterns have practical use: Once they are known, they can provide indicators for ecological monitoring.

Figure 7 shows one of the predictions one might make based on landscape-ecology concepts. If you consider a city in a semi-arid or arid region where water limits natural biotic productivity, you might predict that soil respiration would be more variable in the undisturbed natural ecosystem than in the fringes of an urban area, where water and nutrients are more uniformly supplied for agriculture and suburban residential development. As you move toward the urban core, the fine-scale pattern of land use changes, and you would expect more variability in irrigation from one patch to the next. Therefore in the city's center there is more point-to-point variation than in the natural ecosystem, although along the fringe there is less. Similarly, the natural temporal variation in hydrological conditions might be "smoothed out" by agricultural and horticultural activities along the fringe but might vary more in the center because of extensive modification of hydrology.

As we mentioned before, one of the issues we face is defining what an urban ecosystem is. Having introduced the urban core, the urban fringe and the energy intensity and heterotrophic nature of the city, we can begin to sketch out an emerging view of what an urban ecosystem is. First, we have the advice of the U.S. Census Bureau, which defines an area with a population density over 620 individuals per square kilometer as "urban." We know that these individuals exhibit a high per capita energy consumption and that their habitat is characterized by large-scale environmental modification. But these characteristics are variable. One useful paradigm for viewing them is that of the environmental gradient. Mark McDonnell (then at the Institute for Ecosystem Studies in New York) and colleagues in 1997 showed that urban-rural environmental gradients measuring change in these characteristics can be used to capture the indefinite boundaries of many urban ecosystems. But many other characteristics could be used to do so.

Strange Changes

Like any ecosystem, an urban ecosystem is dynamic and changing. Are the forces that drive change similar to those in a nonurban system? Some clearly are: Disturbances such as fire, flood and earthquake are inevitable in cities. Yet people constantly struggle to control and manage the frequency and magnitude of disturbance. Therefore—although we're not likely to be able to control earthquakes—disturbance regimes are often altered by human action. Separated from the Mississippi River by dikes, New Orleans is protected from much of the flooding that would be its natural disturbance regime.

Likewise, the way an urban ecosystem recovers from a disturbing event may be altered dramatically by human intervention. In nonurban ecosystems a fire or flood is typically followed by a gradual and somewhat predictable series of changes called ecological *succession*. Human intervention may suppress such patterns altogether. An abandoned home site may begin to fill with plant growth—vegetative succession, to an ecologist—but redevelopment typically truncates the process that might otherwise fill the patch with trees and animals. Such redevelopment is an example of the single most important force of landscape change in urban areas: land conversion, driven by institutional decisions, population growth and economic forces.

We generally think of climate change and biological evolution as occurring on much longer time scales than fire and flood—and far longer than the frame of reference for urban ecology. Yet evolutionary and climatic change are likely accelerated or enhanced in urban ecosystems. Figure 8 (bottom) shows examples of species whose evolution has been in-

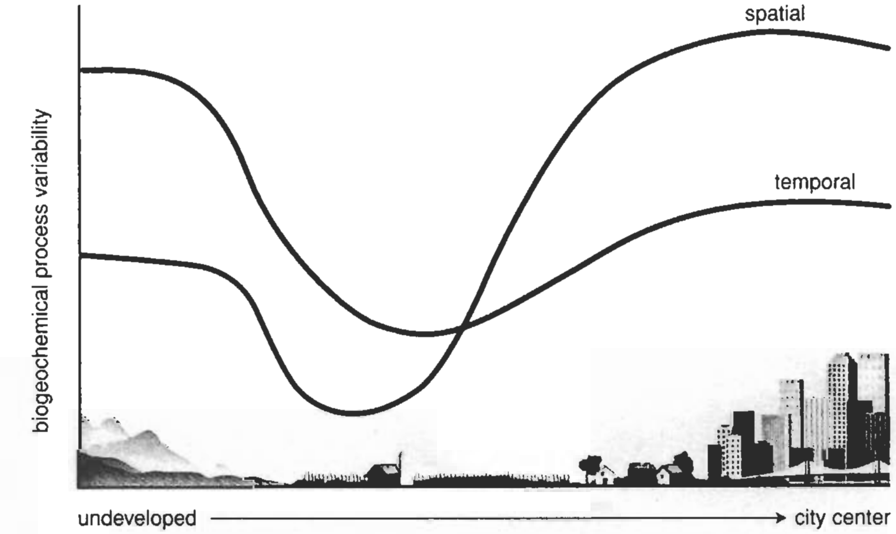
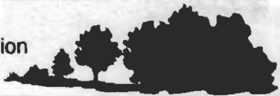


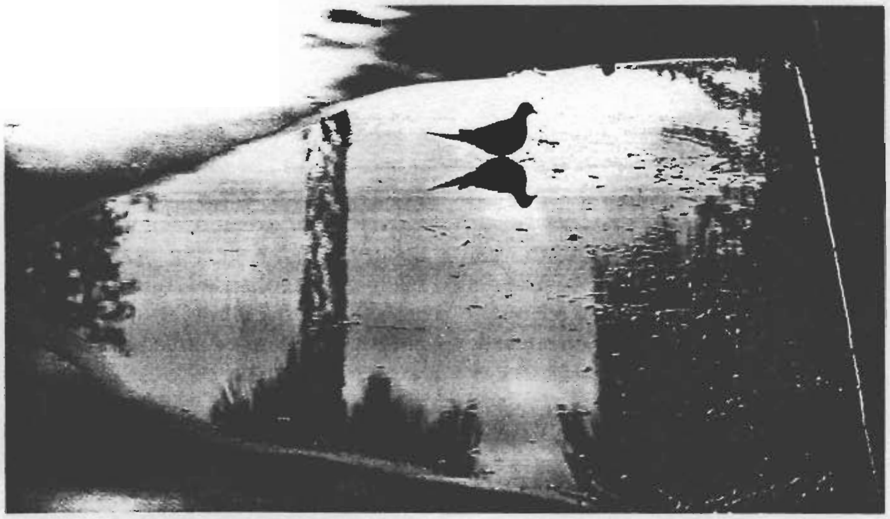
Figure 7. Variability in biogeochemical processes, such as soil respiration, can be high in natural ecosystems. Human activity often smooths out variation, but it can also increase it. Looking along a rural-urban gradient in an arid or semi-arid region, one would expect these processes to vary widely in rural environments over both time and space, since water scarcity limits biological productivity. In the fringe of an urban area, characterized by irrigated agriculture and large-lot-size residential development, the water supply is more constant, reducing variability. Approaching the urban core, the fine-scale patterning of land cover increases; an irrigated park might adjoin an arid expanse of concrete and glass. This might increase point-to-point variability and, to a lesser extent, temporal swings such as those resulting from seasonal flooding.

fluenced by selection pressures created by human activity—often over periods as short as 1 to 30 years. Recent studies have shown that fruit flies and egg-laying butterflies have rapidly adapted to prefer new human-introduced host plants. And in recent decades many organisms placed under strong selection pressure by human action have evolved resistance mechanisms—bacteria to antibiotics, rats to poison, weeds to herbicides. The extreme selective pressures exerted by human environmental changes suggest that evolution in urban ecosystems will likely be evolution under the nonequilibrium conditions of rapidly changing environments. Surviving species in urban ecosystems will be those, such as cockroaches, rats and cats, that cope with anthropogenic selection pressures by rapid evolution or phenotypic plasticity.

The possible effects of urban ecosystems on climate regimes have hardly been investigated, but a few observations suggest they should be. Consider the well-known "urban heat island" effect—the fact that temperatures within cities can exceed those in surrounding areas by several degrees on average. Current research in Phoenix shows that carbon dioxide concentrations within the city center are elevated to several times the global average, a change that has likely taken place on a decadal time scale. How such rapid change within an urban microclimate affects plant, animal and microbial species has hardly been investigated.

In fact, there are findings that suggest that human activity may be capable of altering regional climate patterns in striking ways. In 1998 Randall S. Cerveny and Robert C. Balling, Jr. of Arizona State University demonstrated that the five-day workweek and accompanying commute affected precipitation patterns on the East Coast of the U.S. by making rainfall more likely on weekends than weekdays. In this case the patterns of human activity, unlike those of most animals, did not follow natural rhythms but seemed to alter them. In other cases human activity, of course, has tended to follow natural cycles: We are active by day and sleep by night; throughout human time our festivals have tracked harvests or grown out of the need to fill winter nights. Natural variability in weather and climate can dictate temporal patterns in the organization of society, but it is unclear whether people living in modern urban ecosystems are as likely to develop social rhythms responding to nat-

forces of change in ecosystems		urban ecosystems	temporal scale
disturbance events		suppressed	<1 year
ecological succession		altered, supressed or truncated	1–100 years
disturbance regimes		altered	10–1,000 years
land conversion		dominant	1–100 years
evolutionary change		accelerated	10–1,000 years
climate change		enhanced	100–100,000 years



organism	evolutionary change in . . .
soapberry bugs	capacity to exploit introduced plants
fruit flies	capacity to exploit apple trees
checkerspot butterflies	preference for introduced plants as egg laying and feeding sites
flatworm	host from exotic fish to endangered native fish
bacteria (in humans)	resistance to antibiotics
American house sparrows	mass plus wing and bill lengths
flies	resistance to DDT and other pesticides
rats, other rodents	resistance to poisons

Figure 8. Ecosystems typically undergo changes as a result of disturbance (such as fire or flood) and ecological succession, a series of changes in species composition following disturbance. Climate change and evolutionary factors also promote change. In urban ecosystems the effects of some forces of change are weakened *(top)*, whereas other forces are introduced or enhanced by human activity. Like the mourning dove, many organisms have adapted to life in urban environments or undergone novel evolutionary changes *(table, bottom)* through interactions with people. (Photograph by Nancy McIntyre, Arizona State University; table derived from Thompson 1998, Hendry and Kinnison 1999.)

ural cycles as are rural human societies that depend vitally on a local resource—hunter-gatherer societies or subsistence-agriculture villages, for example.

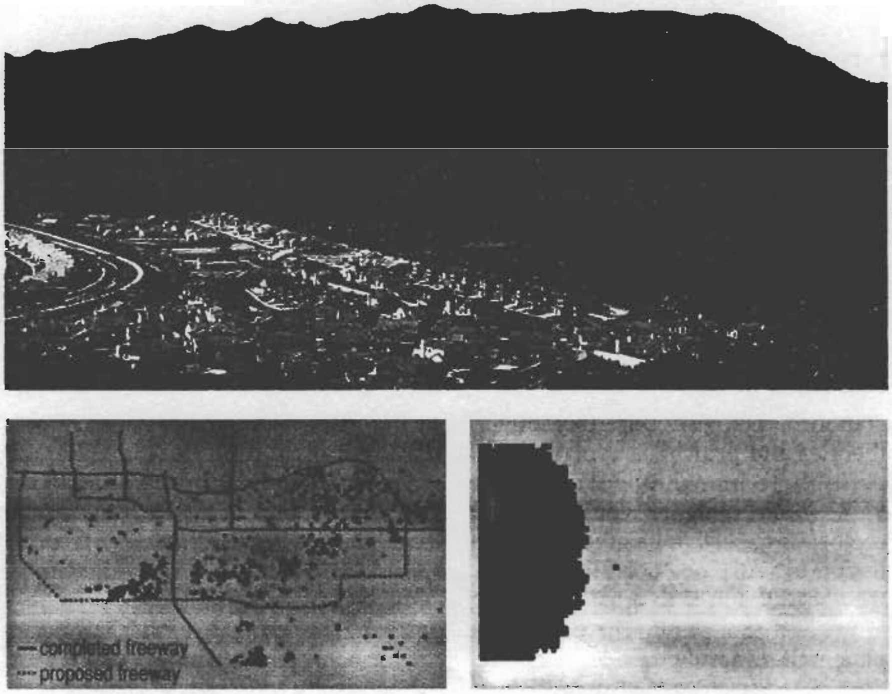
Can ecological theory be extended to study these new forms of change and disturbance? One way to do so is to analogize human disturbance regimes to known ecological regimes. Home construction may be viewed as an ecological disturbance, framing a new question: How does an urban ecosystem recover from such disturbance? Patricia Gober, an ASU geographer participating in the LTER study, and her colleagues viewed the zone of rapid land conversion at the Phoenix urban fringe as a wave of disturbance spreading outward from several urban nodes in the desert alluvial plain. They have calculated land consumption rates and are seeking indicators of incipient urban expansion at the fringe.

And the Cerveny and Balling result is provocative. In ecosystems not dominated by people, individual plants, dispersal distances and the scale of disturbance can define the spatial scales over which processes are influenced and patterns emerge. Both the temporal and spatial scales of patterns in human-dominated ecosystems are likely to emerge from social forces far removed from foraging and dispersal strategies. There are many clear examples of human-imposed spatial scales in our history. The opening of the American West and the Homestead Act enforced a pattern of 160-acre plots on the landscape. Urban ecosystems are usually developed within a grid of blocks each 100 or 200 meters long. Thus we should not be surprised to find new spatial scales emerging for ecological processes within urban systems. However unusual it seems to a landscape ecologist, we are likely to be studying processes on the scales determined by the human-built infrastructure: perhaps the individual homesite, or a city block.

Toward Synthesis

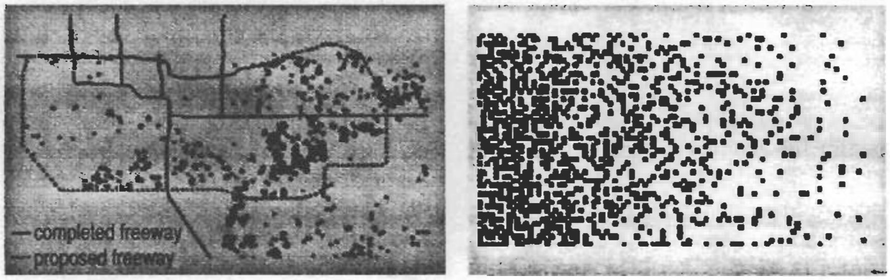
Is there a possibility of simply stretching current ecological theory to encompass urban ecosystems? It can be argued that our understanding of dynamics and processes for populations and soils can be extended to homeowners' associations and pavement. Perhaps the tools already developed for understanding the emergence of different life-history strategies can be extended, without conceptual changes, to people. Human beings, we might argue, are like other organisms. Selective pressures and evolved strategies lead to certain population dynamics and patterns, to certain impacts on surrounding regions and species and finally to certain changes in the allocation or flow of nutrients and resources. It could be that the differences in the ways in which people and other organisms evolve, interact with, and influence their surroundings are merely quantitative, not qualitative.

Or one can take the position that current ecological theory is insufficient to capture the key patterns and processes in these human-dominated or urban ecosystems. Human beings, that is to say, are qualitatively unlike other organisms. The emergence and influence of culture, the constraints and opportunities afforded by our institutions, and our ability to create strategies in response to anticipated (rather than realized) selection pressures mean that



1990 residential completions

model output (clustered development)



1997 residential completions

model output (sprawl)

Figure 9. Growth of the urban fringe in cities such as Phoenix *(photograph)* is an aspect of urban ecology that might be studied by combining the tools of ecology and the social sciences. For instance, a simple ecological model can depict urbanization using housing data. Panels a and b plot the locations of new housing starts in Phoenix and its southeastern suburbs in 1990 and 1997. One can see patterns including "rings" of development and the rapid outward spread of urbanization along some axes. Similar patterns can be generated by simple probabilistic settling models based on the ecological concept of density dependence *(blue panels)*. In such models the density of houses at two radii determines the likelihood of a new house going up, just as one would simulate how a species would colonize a "pristine" ecosystem patch by patch. (Photograph by Ramón Arrowsmith, Arizona State University; data from Maricopa Association of Governments.)

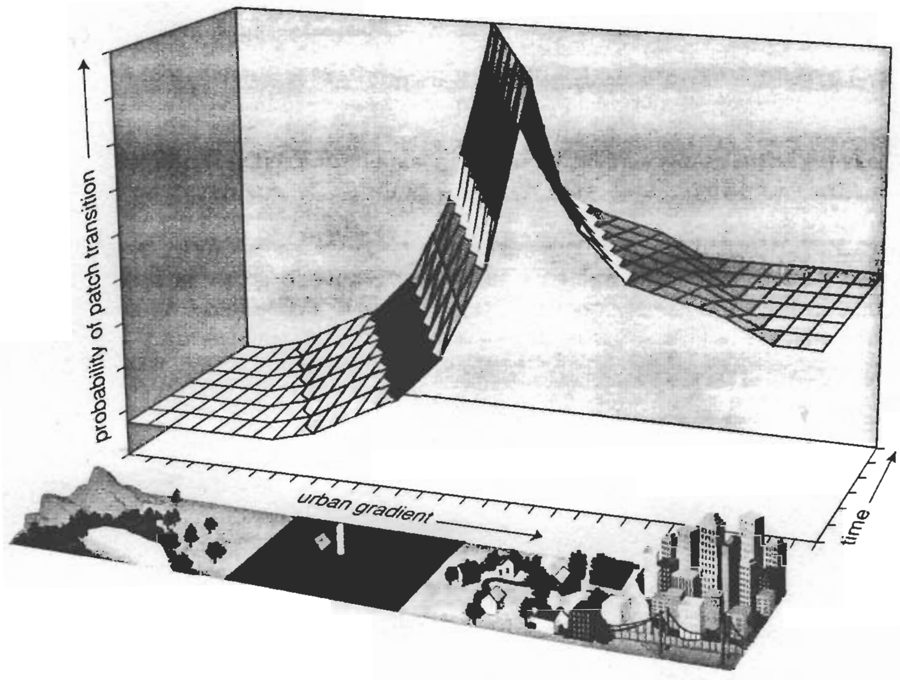


Figure 10. Once an urban area is mapped as a collection of patches, urbanization can be modeled by looking at the probability that a given patch might undergo a transition over time, based on its location along a gradient from rural to urban. Generally the probability of change in the rural environment is relatively low; change is most likely along the urban fringe; and the city center is more stable than the fringe but more likely to experience change than the rural environment. The authors hypothesize that in a typical city a wave of high disturbance radiates through time outward from the initial city edge, as plotted on the graph.

standard ecological and evolutionary theories and principles apply only imperfectly to human populations. This view would obligate would-be urban ecologists to seek out a great deal of interaction with, or "borrowing from," the social sciences to advance ecology in general to a point where it can explain patterns and processes in human-dominated systems.

Either approach implies hard philosophical truths. If a person can be treated as any other organism, the distinction between "natural" and "unnatural" systems disappears, and with it the idea of a "pristine" ecosystem. The whole notion of environmental stewardship may suffer as well. If people act as other organisms do, guided by individual self-interest, there are no grounds for a moral or aesthetic call to stewardship. In the second case, we are forced to face the question of why people are not like other organisms: Is there, for instance, a spiritual or moral dimension that defies explanations offered by evolution or natural selection?

Philosophy aside, it is not clear that any ecologist has to make a hard choice. Standard ecological theories can be and have been applied to human systems; they can be used, for instance, to understand the "dispersal" or "successional dynamics" of urban systems. We can then determine which patterns or details, if any, are impervious to explanations emerging from these standard theories. At the same time, we should examine whether inter- or multidisciplinary approaches between the biological and social sciences provide more elegant theories or explanatory power.

Consider some of the leading conceptual questions mentioned above. How do we study the change in the position or shape of the "urban fringe"—the dynamics of the edge of the city and its expansion? Borrowing tools strictly from ecology, we could begin by employing plant-dispersal and competition models. Thus expansion of the urban fringe could be understood in terms of the density of surrounding neighborhoods, with residences "produced" from nearby "occupied" cells and dispersed to nearby empty cells *(Figure 9)*. One can imagine density-dependent processes controlling neighborhood changes. Another tool is the contact-process model, wherein the probability of a lot undergoing a transition from empty to occupied (with a house) could depend on the "state" of the neighboring lots—whether they are devoted to residential, commercial, agricultural or recreational purposes. Empty cells could be assigned probabilities for colonization based on their own properties, which could vary across the landscape: Is there good drainage, a good view, an adequate groundwater supply?

The processes of urban-fringe expansion also can be described in the ecologists' language of disturbance, as Patricia Gober has. Urbanization at the outer edges of a sprawling metropolis involves both the spatial expansion of human disturbance and the alteration of ecological processes. For any given patch, we can assign a probability of transition (or new disturbance). We might hypothesize that this probability is low in the nonurban matrix, increases steeply at the urban fringe and returns to an intermediate level of disturbance in the center of the city (*Figure 9*). As urbanization of the surrounding matrix proceeds, the probability for patch transition increases in areas that were previously nonurban while decreasing in the former urban-fringe areas, now incorporated into the metropolis. A simple hypothesis derived from these patch-transition probabilities is that a wave of high disturbance radiates through time outward from the initial city edge.

These approaches could help us capture some of the patterns and dynamics of urban-fringe expansion. But what would they be missing? To start with, a dose of economics is surely necessary to explain year-to-year patterns in housing starts. What are the variations in interest rates? In unemployment? In inflation? Economic modeling might predict the number of new houses produced and sold each year, and we could return to ecological theory to examine their dispersal. But there are still more factors to consider. How are decisions for locating roads, establishing sewer lines, or extending emergency services made? How does the power and the approach of state or city institutions change as cities grow? Does the proximity of other municipal organizations affect decisions for developing city boundaries? To capture these effects, we would need to know much more about political theory and the evolution of government institutions.

At this point we would still lack insight into why people value certain spaces over others, or how those values vary by socioeconomic class, family situation and age. For this we may need to turn to sociology to improve our predictions about "dispersal" of houses, and how dispersal patterns might change with economic development, a changing age structure of inhabitants or with new cultural traditions introduced by new arrivals. A return to ecological theory would be required to understand how housing starts affect the landscape, including its biodiversity, and thus potentially alter people's preferences for these sites.

We are still missing information, finally, on how individual and societal preferences vary over time. To take an obvious example of changing preferences, consider the role of the city center in medieval versus modern times. In medieval times, citizens returned to the city center at night for protection. In modern times, we find many inhabitants avoiding the city center at night, again for protection. Similarly, our desires for privacy or large yards or suburban/rural surroundings have changed over the course of this century with changing societal values. Both social sciences and evolutionary biology might provide tools for understanding this "evolution" of culture.

As ecologists, we have begun examining city-fringe expansion with the tools of ecology. Yet we hope that analyzing which patterns and dynamics we fail to capture with this approach will allow us to understand where the most important contributions from the social sciences can be made. Similarly, examining our failure to capture pattern even after incorporating the contributions of the social sciences will help us to understand where a return to the biological basis for the evolution and development of cultures might advance further understanding.

Additional examples of problems that will require multidisciplinary approaches abound. We might want to examine the impact of the urban environment on the distribution and abundance of organisms. The study of island biogeography suggests tools for studying the effects of habitat fragmentation. Evolutionary biology could be invoked to examine variations in selection pressures along urban to rural gradients. But social-science tools are required to explain the preferential cultivation or destruction of some species by the human inhabitants of the city, and how these preferences vary as a function of socioeconomic class, age or place of birth. The presence of exotic species and the increased opportunities for dispersal or invasion caused by habitat disruption and fragmentation would force us to return to the tools of ecology to understand the effects of introduced species on native populations.

Ecological theory might benefit from the use of analogies to accelerate the development of new concepts that can be applied to urban human-ecological systems. Gregg Mitman has discussed how this approach was used in the 1920s and 1930s by University of Chicago sociologists Robert Park and Ernest Burgess and their colleagues and ecologists such as W. C. Allee, Alfred Emerson and Thomas Park to develop ideas of "human sociality." These were the early urban ecologists who attempted to understand human actions by analogy with ecological systems. Although we recognize the danger inherent in its indiscriminate use, comparison of succession and urbanization reveals the heuristic utility of this kind of analogy. In a city with spreading growth, the perimeter or "urban fringe" can be viewed as an active disturbance area, and locations farther removed from the fringe (inward) as earlier in succession (space-for-time substitution).

William Cronon, an environmental historian, argued that the disciplines of ecology, history, geography, anthropology and others could "learn from one another if only we can scale the walls that separate us to start working together on the problems we all find fascinating." The challenge of understanding urban ecosystems will require disciplinary specialists, but it will also require at least some individuals willing to think in interdisciplinary and multidisciplinary ways—a task that can be difficult to accomplish. These investigators will have to knock down the walls, rather than scale them, to integrate diverse disciplines into a synthetic research area and a novel perspective that will advance ecological theory. Urban ecosystems afford a distinctive model for developing and testing such an integrative perspective.

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are available on the
American Scientist Web site:
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