

URBAN ECOLOGICAL SYSTEMS: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas*

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■ **Abstract** Ecological studies of terrestrial urban systems have been approached along several kinds of contrasts: ecology in as opposed to ecology of cities; biogeochemical compared to organismal perspectives, land use planning versus biological, and disciplinary versus interdisciplinary. In order to point out how urban ecological studies are poised for significant integration, we review key aspects of these disparate literatures. We emphasize an open definition of urban systems that accounts for the exchanges of material and influence between cities and surrounding landscapes. Research on ecology in urban systems highlights the nature of the physical environment, including urban climate, hydrology, and soils. Biotic research has studied flora, fauna, and vegetation, including trophic effects of wildlife and pets. Unexpected interactions among soil chemistry, leaf litter quality, and exotic invertebrates exemplify the novel kinds of interactions that can occur in urban systems. Vegetation and faunal responses suggest that the configuration of spatial heterogeneity is especially important in urban systems. This insight parallels the concern in the literature on the ecological dimensions of land use planning. The contrasting approach of ecology of cities has used a strategy of biogeochemical budgets, ecological footprints, and summaries of citywide species richness. Contemporary ecosystem approaches have begun to integrate organismal,

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nutrient, and energetic approaches, and to show the need for understanding the social dimensions of urban ecology. Social structure and the social allocation of natural and institutional resources are subjects that are well understood within social sciences, and that can be readily accommodated in ecosystem models of metropolitan areas. Likewise, the sophisticated understanding of spatial dimensions of social differentiation has parallels with concepts and data on patch dynamics in ecology and sets the stage for comprehensive understanding of urban ecosystems. The linkages are captured in the human ecosystem framework.

INTRODUCTION: JUSTIFICATION FOR URBAN ECOLOGICAL STUDIES

Urbanization is a dominant demographic trend and an important component of global land transformation. Slightly less than half of the world's population now resides in cities, but this is projected to rise to nearly 60% in the next 30 years (United Nations 1993). The developed nations have more urbanized populations; for example, close to 80% of the US population is urban. Urbanization has also resulted in a dramatic rise in the size of cities: over 300 cities have more than 10^6 inhabitants and 14 megacities exceed 10^7 . The increasing population and spatial prominence of urban areas is reason enough to study them, but ecologists must also inform decision makers involved in regional planning and conservation. Proper management of cities will ensure that they are reasonable places to live in the future.

In addition to its global reach, urbanization has important effects in regional landscapes. For example, in industrialized nations, the conversion of land from wild and agricultural uses to urban and suburban occupancy is growing at a faster rate than the population in urban areas. Cities are no longer compact, isodiametric aggregations; rather, they sprawl in fractal or spider-like configurations (Makse et al. 1995). Consequently, urban areas increasingly abut and interdigitate with wild lands. Indeed, even for many rapidly growing metropolitan areas, the suburban zones are growing faster than other zones (Katz & Bradley 1999). The resulting new forms of urban development, including edge cities (Garreau 1991) and housing interspersed in forest, shrubland, and desert habitats, bring people possessing equity generated in urban systems, expressing urban habits, and drawing upon urban experiences, into daily contact with habitats formerly controlled by agriculturalists, foresters, and conservationists (Bradley 1995).

Urban habitats constitute an open frontier for ecological research. Ecologists have come to recognize that few ecosystems are totally devoid of direct or subtle human influence (McDonnell & Pickett 1993). Yet urban systems are relatively neglected as an end member with which to compare the role of humans in ecosystems. Notably, many classic geographic studies of cities, which offer valuable insights to ecologists, are based on outmoded ecological theory such as deterministic models of succession and assumptions of equilibrium dynamics of ecosystems. Hence

classical ecological approaches and the geographic studies that have relied on them have not been as useful as they would be otherwise (Zimmerer 1994).

Although the ecology of urban areas has long elicited the academic attention of ecologists, physical and social scientists, and regional planners, there is much opportunity to extend and integrate knowledge of the metropolis using an ecological lens. The purpose of this paper is to review the status of ecological knowledge of the terrestrial components of urban areas and to present a framework for continued ecological research and integration with social and economic understanding. This paper complements the review of aquatic components of urban systems by Paul & Meyer (2001).

Definition and Roots of Urban Ecology

Urban ecosystems are those in which people live at high densities, or where the built infrastructure covers a large proportion of the land surface. The US Bureau of the Census defines urban areas as those in which the human population reaches or exceeds densities of 186 people per km². However, an ecological understanding of urban systems also must include less densely populated areas because of reciprocal flows and influences between densely and sparsely settled areas. Comparisons along gradients of urbanization can capture the full range of urban effects as well as the existence of thresholds. Therefore, in the broadest sense, urban ecosystems comprise suburban areas, exurbs, sparsely settled villages connected by commuting corridors or by utilities, and hinterlands directly managed or affected by the energy and material from the urban core and suburban lands.

The boundaries of urban ecosystems are often set by watersheds, airsheds, commuting radii, or convenience. In other words, boundaries of urban ecosystems are set in the same ways and for the same reasons as are the boundaries in any other ecosystem study. In the case of urban ecosystems, it is clear that many fluxes and interactions extend well beyond the urban boundaries defined by political, research, or biophysical reasons. Urban ecology, as an integrative subdiscipline of the science of ecology, focuses on urban systems as broadly conceived above. There is little to be gained from seeking distinctions between “urban” and abutting “wild” lands, as a comprehensive, spatially extensive, systems approach is most valuable for science (Pickett et al. 1997) and management (Rowntree 1995).

There are two distinct meanings of urban ecology in the literature (Sukopp 1998). One is a scientific definition, and the other emerges from urban planning. In ecology, the term urban ecology refers to studies of the distribution and abundance of organisms in and around cities, and on the biogeochemical budgets of urban areas. In planning, urban ecology has focused on designing the environmental amenities of cities for people, and on reducing environmental impacts of urban regions (Deelstra 1998). The planning perspective is normative and claims ecological justification for specific planning approaches and goals. We review key aspects of these complementary approaches and then frame a social-ecological approach to integrate these two approaches.

BIOGEOPHYSICAL APPROACHES

There are two aspects to the biogeophysical approach to urban ecological studies. One, the pioneering and most common approach, examines ecological structure and function of habitats or organisms within cities. This approach is called ecology in cities. The second, more recent and still emerging approach, examines entire cities or metropolitan areas from an ecological perspective. The second approach is labeled ecology of cities (Grimm et al. 2000). Although the differences in the prepositions in the phrases identifying the two contrasting approaches may appear subtle, the understanding achieved by identifying them as poles between which urban ecological studies sort out, is crucial to understanding the history of urban ecology, and the integration it is now poised to make. We review literature that has taken these two contrasting approaches in turn.

Ecology in the City

The study of ecology in the city has focused on the physical environment, soils, plants and vegetation, and animals and wildlife. These studies are the foundation for understanding urban ecosystems. The literature in this area has taken a case study approach, and unifying themes are still to emerge. We highlight key examples from among the many cases.

URBAN PHYSICAL ENVIRONMENT The urban heat island constitutes climate modification directly related to urban land cover and human energy use (Oke 1995). The urban heat island describes the difference between urban and rural temperatures. Such differences often are negligible in the daytime but develop rapidly after sunset, peaking 2–3 h later. Ambient air temperatures may reach maxima of 5–10°C warmer than hinterlands (Zipperer et al. 1997). For example, New York City is, on average, 2–3°C warmer than any other location along a 130-km transect into surrounding rural areas (McDonnell et al. 1993). The duration and magnitude of the temperature differential depend on the spatial heterogeneity of the urban landscape. As the percentage of artificial or human-made surfaces increases, the temperature differential increases. Hence, the urban core is warmer than neighboring residential areas, which are warmer than neighboring farmlands or forests. The differences also change seasonally. For example, cities in mid-latitudes of the United States are typically 1–2°C warmer than the surroundings in winter, and 0.5–1.0°C warmer in summer (Botkin & Beveridge 1997).

The heat island effect varies by region, as seen in a comparison between Baltimore, Maryland, and Phoenix, Arizona (Brazel et al. 2000). During the summer, mean maximum temperatures in Baltimore were greater than in the rural landscape. Phoenix, on the other hand, became an oasis, with cooler temperatures than the surrounding desert. The cooling of Phoenix is due to the watering of mesic plantings in the city. In contrast, the mean minimum temperatures were warmer in both cities than in the respective neighboring rural landscape, although the differential in Phoenix was greater.

The heat island intensity also is related to city size and population density (Oke 1973, Brazel et al. 2000). For example, Baltimore's mean minimum temperature differential increased until the 1970s when the city experienced a decline in population. Since 1970, the mean minimal temperature differential has leveled off. Phoenix also showed an increase in mean minimum temperature differential with an increase in population. However, Phoenix is the second fastest growing metropolitan area in the United States, so the differential has continued to increase with population growth. In general, a nonlinear relationship exists between mean minimum temperature differential and population density (Brazel et al. 2000).

The differences in climate between city and countryside have biological implications. For example, as a result of climatic modification in temperate zone cities, leaf emergence and flowering times are earlier, and leaf drop is later than in the surrounding countryside (Sukopp 1998). Increased temperatures in and around cities enhance ozone formation, and increase the number of officially recognized pollution days and trace gas emissions (Sukopp 1998). Ozone concentrations tend to be highest in and around urban areas. As urban areas have expanded through processes of suburban sprawl, the spatial influence of urbanization has increased. Within regions of ozone pollution, agricultural crops may be adversely affected and yields decrease 5–10% (Chameides et al. 1994). Crop type and stage of development, and the degree, spatial extent, and duration of ozone exposure may all influence the decrease in production (Chameides et al. 1994).

Precipitation is enhanced in and downwind of cities as a result of the higher concentrations of particulate condensation nuclei in urban atmospheres. Precipitation can be up to 5–10% higher in cities, which can experience greater cloudiness and fog (Botkin & Beveridge 1997). The probability of precipitation increases toward the end of the work week and on weekends due to a buildup of particulates resulting from manufacturing and transportation (Collins et al. 2000).

Urban hydrology is drastically modified compared to agricultural and wild lands. This topic is covered more fully in a companion review (Paul & Meyer 2001). Relativizing a water budget to 100 units of precipitation, and comparing urban to nonurban areas, evapotranspiration decreases from a value of 40% to 25%, surface runoff increases from 10% to 30%, and groundwater decreases from 50% to 32% (Hough 1995). Forty-three percent of precipitation exits the urban area via storm sewers, with 13% of that having first fallen on buildings. The role of impervious surfaces is crucial to the functioning of urban watersheds (Dow & DeWalle 2000). The hydrology in urban areas can be further modified by ecological structures. For example, reduced tree cover in urban areas increases the rate of runoff and decreases the time lag between initiation of storms and initiation of runoff (Hough 1995). The increased runoff in urban areas changes the morphology of urban streams, which become deeply incised in their floodplains. Remnant riparian vegetation may suffer as a result of isolation from the water table.

URBAN SOILS Soils in urban landscapes retain and supply nutrients, serve as a growth medium and substrate for soil fauna and flora, and absorb and store water.

Soils also intercept contaminants such as pesticides and other toxics generated through human activities (Pouyat & McDonnell 1991). However, in urban settings soils are modified by human activity and, consequently, are functionally altered (Effland & Pouyat 1997). In addition, completely new substrates are created by deposition of debris, soil, and rock in urban sites. Such new substrates are called made land.

As land is converted to urban use, both direct and indirect factors can affect the functioning of soils. Direct effects include physical disturbances, burial of soil by fill material, coverage by impervious surfaces, and additions of chemicals and water (e.g., fertilization and irrigation). Direct effects often lead to highly modified substrates in which soil development then proceeds (Effland & Pouyat 1997). Indirect effects change the abiotic and biotic environment, which in turn can influence soil development and ecological processes in intact soils. Indirect effects include the urban heat island (Oke 1995), soil hydrophobicity (White & McDonnell 1988), introductions of nonnative plant and animal species (Airola & Buchholz 1984, Steinberg et al. 1997), and atmospheric deposition of pollutants (Lovett et al. 2000). Moreover, toxic, sublethal, or stress effects of the urban environment on soil decomposers and primary producers can significantly affect the quality of organic matter and subsequent soil processes (Pouyat et al. 1997).

The results from a transect along an urban-rural land-use gradient in the New York City metropolitan area show the influence of urban environments on intact forest soils (McDonnell et al. 1997). Along this transect, human population density, percent impervious surface, and automobile traffic volume were significantly higher at the urban than the rural end of the gradient (Medley et al. 1995). Soil chemical and physical properties, soil organism abundances, and C and N processes were investigated along this gradient to assess the sometimes complex and sometimes contradictory interactions between urban soil chemistry, local leaf litter quality, and exotic species.

Soil chemistry significantly correlated with measures of urbanization. Higher concentrations of heavy metals (Pb, Cu, Ni), organic matter, salts, and soil acidity were found in the surface 10 cm of forest soils at the urban end of the transect (Pouyat et al. 1995). The most probable factor is metropolitan-wide atmospheric deposition.

Litter decomposition studies in both the field and the laboratory determined that urban-derived oak litter decomposed more slowly than rural-derived oak litter under constant conditions (Carreiro et al. 1999), with lignin concentration explaining 50% of the variation. Moreover, a site effect was measured for reciprocally transplanted litter, as decomposition was faster in the urban than in the rural sites, regardless of litter origin. This result is surprising because the lower litter fungal biomass and microinvertebrate abundances found in urban stands compared to rural (Pouyat et al. 1994) would lead to an expectation of slower litter turnover rates in urban forests. However, abundant earthworms (Steinberg et al. 1997) and higher soil temperatures in the urban stands may compensate for lower litter quality, lower fungal biomass, and lower microinvertebrate abundances in the urban stands

(R.V. Pouyat & M.M. Carreiro, submitted for publication). Such compensation likely explains the faster decomposition rates in the urban stands.

Litter quality, site environment, and soil organism differences between the urban and rural sites also affected C and N pools and processes in the soil. Urban litter was found to be of lower quality (higher C:N ratio) than rural litter. Typically, poor quality litter either decreases the rate at which labile C mineralizes N or increases the amount of organic matter transferred to recalcitrant pools, or both. Hence, urban litter is expected to be more recalcitrant than rural litter. Indeed, measurements of soil C pools along the urban-rural transect suggest that recalcitrant C pools are higher and passive pools lower in urban forest soils relative to rural forest soils (Groffman et al. 1995). Consequently, N mineralization rates were expected to be lower in urban stands. However, the opposite was found. Net potential N-mineralization rates in the A-horizon were higher in the urban stands than in the rural stands (Pouyat et al. 1997). Soil cores taken from urban areas accumulated more NH_4^+ and NO_3^- than soil from rural areas. In addition, from a reciprocal transplant experiment, soil cores incubated at urban sites accumulated more inorganic N than cores incubated at the rural sites, regardless of where the cores originated. These net N mineralization rates contradict both the litter decomposition results from the transplant experiment discussed above and expectations derived from measurements of soil C pools.

In contrast, when net N-mineralization rates were measured for mixed O, A, and B horizon material (15 cm depth), the total inorganic N pool accumulated was higher in rural than in urban sites, although less NO_3^- was accumulated in rural samples (Goldman et al. 1995). The mechanisms behind these results have yet to be elucidated, though it has been hypothesized that methane consumption rates and the biomass of methanotrophs are important regulators in overall soil C and N dynamics (Goldman et al. 1995).

Intense soil modifications resulting from urbanization may potentially alter soil C and N dynamics. To assess the potential effect on soil organic C, data from "made" soils (1 m depth) from five different cities, and surface (0–15 cm) soils from several land use types in Baltimore were analyzed (R.V. Pouyat, P.M. Groffman, I. Yesilonis & L. Hernandez, submitted for publication). Soil pedons from the five cities showed the highest soil organic C densities in loamy fill (28.5 kg m^{-2}) with the lowest in clean fill and old dredge materials (1.4 and 6.9 kg m^{-2} , respectively). Soil organic C for residential areas ($15.5 \pm 1.2 \text{ kg m}^{-2}$) was consistent across cities. A comparison of land-use types showed that low density residential and institutional land had 44% and 38% higher organic C densities than commercial land, respectively. Therefore, made soils, with their physical disturbances and inputs of various materials by humans, can greatly alter the amount of C stored in urban systems.

The complex patterns of C and N dynamics that have emerged from the studies reviewed above indicate interactions between key soil and organism processes in urban environments. Simple predictions based on trends in pollution, stress, or exotic species alone are inadequate to understand the complex feedbacks between

these three governing factors of urban soil dynamics. Studies of soil C and N dynamics in unmanaged urban forests, highly disturbed soils, and surface soils of various urban land-use types all show that urbanization can directly and indirectly affect soil C pools and N-transformation rates. Our review also suggests that soil C storage in urban ecosystems is highly variable. How generalizable these results are across cities located in similar and dissimilar life zones needs to be investigated. In addition, more data are needed on highly disturbed soils, such as landfill, managed lawns, and covered soils to make regional and global estimates of soil C storage and N-transformation rates in urban ecosystems. Specific uncertainties include the quality of the C inputs governed by the input of litter from exotic plant species and by stress effects on native species litter, the fate of soil C in covered soils, measurements of soil C densities at depths greater than 1 m, particularly in made soils, and the effects of specific management inputs on N-transformation rates.

VEGETATION AND FLORA IN CITIES The assessment of vegetation in urban landscapes has a long history. For example, in Europe, studies by De Rudder & Linke (1940) documented the flora and fauna of cities during the early decades of the twentieth century. After World War II, Salisbury (1943) examined vegetation dynamics of bombsites in cities. At the same time, ecologists in the United States focused on describing flora in areas of cities minimally altered by humans, such as parks and cemeteries. One of the first comprehensive studies of urban vegetation and environments was conducted by Schmid (1975) in Chicago.

The structure and composition of vegetation has been one of the foci of ecological studies in cities, and these studies have documented large effects of urbanization on forest structure. Urban stands tend to have lower stem densities, unless those stands are old-growth remnants in large parks or former estates (Lawrence 1995). In the Chicago region, street trees and residential trees tend to be larger than those in forest preserves, natural areas, and wild lands (McPherson et al. 1997), although individual trees in urban sites are often stressed, especially on or near streets (Ballach et al. 1998). Street trees in Chicago account for 24% of the total Leaf Area Index (LAI) and 43.7% of the LAI in residential areas (Nowak 1994). In mesic forest regions of the United States, tree cover of cities is approximately 31%, compared to the nearly continuous forest cover the areas would have supported before settlement. Brooks & Rowntree (1984) quantified the forest cover in counties classified as nonmetropolitan, peripheral to a central city, and encompassing a central city. They found that the proportion of total land area in forest decreased from nonmetropolitan to central city counties, with the steepest reductions between nonmetropolitan and peripheral counties. In contrast, for prairie-savanna and desert regions, tree cover in cities is greater than in pre-urban conditions (Nowak et al. 1996).

There are also local effects on urban vegetation. For example, forest patches adjacent to residential areas have increased edge openness (Moran 1984), and their margins have retreated because of recreational use, especially by children, and damage to regeneration (Bagnall 1979). Such regeneration failure is frequent in

urban and suburban stands, owing to reduced natural disturbance or gap formation, substitution for natural disturbances of unfavorable anthropogenic disturbances such as frequent ground fires, trampling, and competition with exotics (Guilden et al. 1990).

The composition of urban and suburban forests differs from that of wild and rural stands in several ways. Species richness has increased in urban forests as a whole, but this is because of the increased presence of exotics (Zipperer et al. 1997). Urban areas show a preponderance of trees of wetland or floodplain provenance, owing to the lower oxygen tensions shared by wetlands and impervious urban soils (Spirn 1984). Even when the tree composition remains similar between urban and rural forests, the herbaceous flora of urban forests is likely to differ between the two types of forest (Wittig 1998). Such compositional trends reflect the context and configuration of the forest stands in urban areas. For example, vascular plant diversity increases with the area of the stand (Iida & Nakashizuka 1995, Hobbs 1988). Furthermore, in some urban stands, the adjacent land use affects species composition. For example, the interior of forests in residential areas often has more exotics than forests abutting either roads or agricultural zones (Moran 1984).

The role of exotic species has received particular attention in urban studies. The percentage of the flora represented by native species decreased from urban fringes to center city (Kowarik 1990). Along the New York City urban-to-rural gradient, the number of exotics in the seedling and sapling size classes of woody species was greater in urban and suburban oak-dominated stands (Rudnický & McDonnell 1989). Rapoport (1993) found the number of noncultivated species decreased from fringe toward urban centers in several Latin American cities for various reasons exemplified in different cities. In Mexico City, there was a linear decrease in the number of species from 30–80 ha⁻¹ encountered in suburbs to 3–10 ha⁻¹ encountered in the city center. The social context also influenced species richness. At a given housing density, more affluent neighborhoods had more exotic species than less affluent ones in Bariloche, Argentina. In Villa Alicura, Argentina, exotic species increased with increasing local site alteration by humans. Near homes there were 74% exotics, while there were 48% along river banks. Although exotics were present along all roads, the number decreased on roads less frequently used. No exotic species were found outside the town. Pathways in rural recreation areas (Rapoport 1993) and in urban parks (Drayton & Primack 1996) have enhanced the presence of exotics. In an urban park in Boston, of the plant species present in 1894, 155 were absent by 1993, amounting to a decrease from 84% to 74% native flora. Sixty-four species were new. In addition to trails, Drayton & Primack (1996) blamed fire and trampling for the change in exotics.

Structural and compositional changes are not the only dynamics in urban biota. Plants and animals in cities have evolved in response to the local conditions in cities (Sukopp 1998, Bradshaw & McNeilly 1981). The famous population genetic differentiation in copper and zinc tolerance in creeping bent grass (*Agrostis stolonifera*) and roadside lead tolerance of ribwort plantain (*Plantago lanceolata*) in urban sites is an example (Wu & Antonovics 1975a, b). Industrial melanism and

other forms of melanism are also urban evolutionary responses (Bishop & Cook 1980).

A major feature of urban vegetation is the spatial heterogeneity in urban landscapes created by the array of building densities and types, different land uses, and different social contexts. To characterize this heterogeneity, plant habitats have been subjected to various classification systems. Forest Stearns (Stearns 1971), one of the first American ecologists to call for research in urban landscapes, identified three major vegetation types—ruderal, managed, and residual. In addition to assessing spatial heterogeneity, classification systems recognize the importance of characterizing natural habitats in urban landscapes. Rogers & Rowntree (1988) developed a system to classify vegetation using life forms. This process was used to assess natural resources in New York City (Sisinni & Emmerich 1995). Based on site histories, Zipperer et al. (1997) classified tree-covered habitats as planted, reforested, or remnant. These approaches allow for spatially explicit comparisons between vegetation and other variables of interest for a single point in time.

The vegetation and floristic studies of nature in cities share key characteristics. They are largely descriptive, but illustrate spatial heterogeneity as a source of diversity, and suggest a functional role for landscape structure (Rebele 1994). Although it is legitimate to view the city as an open and dynamic ecosystem, few of the plant ecological studies document successional processes (Matlack 1997) or expose the functional relationships of the vegetation (Mucina 1990).

ANIMALS AND WILDLIFE Douglas (1983), Gilbert (1989), VanDruff et al. (1994), and Nilon & Pais (1997) have summarized the literature on the animal life of cities. They reveal a long history of research on the fauna of European and North American cities. Although much of the research has been descriptive, several studies focused on processes that are also major foci of research in ecology as a whole. We review animal studies starting with coarse scale or gradient comparisons, followed by patch-oriented studies, including some that incorporate socioeconomic aspects, then show how wildlife biologists have contributed to urban ecology, and end with several examples of process studies involving animals.

Birds, mammals, and terrestrial invertebrates are the best studied taxonomic groups, with aquatic fauna, reptiles, and amphibians less studied (Luniak & Pisarski 1994). In addition, the fauna of green spaces are relatively well studied, with built-up and derelict areas and water bodies less well known. Andrzejewski et al. (1978) and Klausnitzer & Richter (1983) described how urban-to-rural gradients defined by human population density and building density impact the occurrence and abundance of various animal species. Among mammals, there is a shift to medium sized, generalist predators such as raccoons and skunks in urban areas (Nilon & Pais 1997). The predator fauna contrasts between cities and nonurban environments. For example, ants were the most important predators in some urban areas although vertebrates were more significant in nonurban habitats (Wetterer 1997). Changes in fauna may influence vegetation. For example, invertebrate pest densities increased in urban trees compared to wild forest stands, reflecting the

additional stress and damage to which urban trees are subjected (Nowak & McBride 1992).

Animal ecologists have recognized spatial heterogeneity in a variety of ways. Heterogeneity is typically expressed as patches or contrasting biotopes. The approach to spatial heterogeneity of urban fauna in Germany has been shaped by a national program of biotope mapping (Sukopp 1990, Werner 1999). The German biotope approach is based on phytosociologic-floristic and faunal characteristics of sites in cities (Sukopp & Weiler 1988). Biotope mapping can be used to document dynamics of urban fauna such as the changes in the bird species composition, and abundance of different types of biotopes (Witt 1996). Brady et al.'s (1979) general typology of urban ecosystems and Matthews et al.'s (1988) habitat classification scheme for metropolitan areas in New York State are examples of schemes that recognize how patterns of land-use history and resulting changes in land cover create ecologically distinct habitat patches.

Use of patch-oriented approaches is particularly well developed in studies of mammals. For example, land use and cover in 50-ha areas surrounding patches in Syracuse, New York, were the best predictors of small mammal species composition (VanDruff & Rowse 1986). Similarly, patch configuration in Warsaw, Poland, affected mammal populations. Urbanization blocked the dispersal of field mice and altered population structure and survivorship in isolated patches (Andrzejewski et al. 1978). Larger mouse populations were associated with increased percentages of built and paved areas, barriers to emigration, and decreases in patch size (Adamczewska-Andrzejewski et al. 1988). In addition, mammalian predators of seeds may be increased in urban patches compared to rural areas (Nilon & Pais 1997). The change in patch configuration resulting from suburban sprawl has led to the widespread increase in deer densities on urban fringes. Suburbanization has caused increased juxtaposition of forest habitats in which deer shelter with field or horticultural patches in which they feed (Alverson et al. 1988). The positive feedback of changing patch configuration on deer population density is magnified by reduced hunting and predator pressure associated with suburbanization. Greater deer densities have the potential to change both the animal community and vegetation (Bowers 1997).

Some biologists have looked to social causes of animal and plant distribution and abundance in cities. Studies of flora and fauna of metropolitan Liverpool, England, showed that changes in land use and technology have influenced habitat change since the industrial revolution (Greenwood 1999), and studies of fauna in suburban Warsaw included land-use information dating from the 1700s (Mackin-Rogalska et al. 1988). Key to the Warsaw study was the recognition that suburban areas have different socioeconomic processes than do either urban or rural areas, and that these processes influence land use, land-cover characteristics, and habitats for biota. Examples of the relationships of animal populations to land-cover types include those for birds. For a city as a whole, exotic generalists such as pigeons, starlings, and sparrows can constitute 80% of the bird community in the summer, and 95% in winter (Wetterer 1997). At finer scales, contrasting land-cover patches of

residential areas, commercial sites, and parks supported different avian assemblages (Nilon & Pais 1997). Even differences in plant cover among residential neighborhoods affected bird community composition. Likewise, the land uses adjacent to urban green spaces strongly influence bird communities (Nilon & Pais 1997).

In Europe and North America, much of the research on the fauna of cities has been conducted by applied ecologists to support conservation and natural resource management. This work recognized that cities are areas worthy of study, and more importantly, that people and their activities create a unique context for natural resource management in and around cities (Waggoner & Ovington 1962, Noyes & Progulské 1974). In particular, the patch dynamics approach was foreshadowed by wildlife ecologists in cities. The activity of urban wildlife biologists is illustrated by the conferences of the National Institute for Urban Wildlife (Adams & Leedy 1987, 1991, Adams & VanDruff 1998). These conferences focused on (a) ecology of urban wildlife, (b) planning and design, (c) management issues and successes, and (d) public participation and education. The participatory approach to studying animals in cities involves urban residents in the process (Adams & Leedy 1987) and serves as a model for other ecological research in cities. Furthermore, the conferences focused on planning and management as activities that can change habitats at both citywide and local scales.

An additional stress on animal populations in cities is the direct or indirect effect of domestic pets. Building density is associated with an increase in the numbers of pets in an area (Nilon & Pais 1997). The amount of food energy available to free-ranging domestic cats depends on the affluence of the immediate neighborhood (Haspel & Calhoun 1991). Cats have a significant impact on bird populations in suburbs (Churcher & Lawton 1987).

An example of an ecological process familiar in wild and production landscapes that also appears in cities is animal succession. After the establishment of the new town of Columbia, Maryland, birds such as bobwhite and mourning dove, which are associated with agriculture, gave way to starlings and house sparrows, which had been absent before urbanization (Hough 1995). In an urban park near Dortmund, Germany, a 35-year study found an increase in generalist species richness and density at the expense of specialists. The species turnover rate of birds in the park between 1954 and 1997—42.1%—was higher than in a forest distant from the city over the same period (Bergen et al. 1998).

This overview of animals in urban areas has confirmed the diversity of exotic and native species in cities. These species, along with the planted and volunteer vegetation in cities, are in some cases an important amenity, and in others a significant health or economic load. They can serve to connect people with natural processes through educational activities. Although there is a great deal of descriptive knowledge about the biota of cities, there is the need to compare food web models for green and built parts of the city, to link these data with ecosystem function, and to quantify the relationships between infrastructural and human behavioral features of the metropolis (Flores et al. 1997). In addition, long-term studies are required.

The case studies we report here are a foundation for generalizations concerning the structure and function of biota within cities.

Ecology of the City

The knowledge of nature in cities is a firm foundation for understanding ecological processes in metropolitan areas. Yet it is not sufficient (Flores et al. 1997). If scientists, planners, and decision makers are to understand how the social, economic, and ecological aspects of cities interact, the feedbacks and dynamics of the ecological linkages must be assessed. We therefore turn to a review of systems-oriented approaches to urban ecology. These represent a shift to the perspective of ecology of cities, as contrasted with the literature we have reviewed so far, which focused on ecology in cities.

The diverse spatial mosaics of metropolitan areas present a variety of ecological situations in which to examine ecological structure and dynamics. For example, several of the conditions in cities are analogous to major predictions of global climate change. Increased temperatures, altered rainfall patterns, and drying of soils anticipate trends projected for some wild lands. Examination of existing urban assemblages or experimentation with novel assemblages of native and exotic species may be useful for assessing the effects of climate change on biodiversity. The stranded riparian zones of urban sites, resulting from the downcutting of streams associated with impervious surfaces, can be used to examine altered environmental drivers of system function. Plant community regeneration and the response of ecosystems to soil nitrogen cycling under altered moisture and temperature conditions may be investigated in such areas. Examining succession in vacant lots may inform practical vegetation management and suggest strategies for changing land use as the density of humans and buildings decline in some city centers. Finally, patterns of adjacency of managed and wild patches in and around cities can be used to examine landscape function.

The ecology of the entire city as a system is represented by research relating species richness to the characteristics of cities. For instance, the number of plant species in urban areas correlates with the human population size. Species number increases with log number of human inhabitants, and that relationship is stronger than the correlation with city area (Klotz 1990). Small towns have from 530 to 560 species, while cities having 100,000 to 200,000 inhabitants have upwards of 1000 species (Sukopp 1998). The age of the city also affects the species richness; large, older cities have more plant species than large, younger cities (Sukopp 1998, Kowarik 1990). These plant assemblages are characteristic throughout Europe, with 15% of species shared among cities (Sukopp 1998).

BIOGEOPHYSICAL BUDGETS One of the earliest modern ecological approaches to urban systems was the assessment of biogeochemical budgets of whole cities (Odum & Odum 1980). It is clear that urban areas are heterotrophic ecosystems that depend on the productivity from elsewhere (Collins et al. 2000). Cities in industrial

countries may use between 100,000 and 300,000 Kcal m⁻² yr⁻¹, whereas natural ecosystems typically expend between 1,000 and 10,000 Kcal m⁻² yr⁻¹ (Odum 1997). The energy budgets of cities are driven by fossil fuel subsidies, which contribute to the urban heat island effect.

How the green component of cities affects biogeochemical processing for the city as a whole has been examined. For example, in Chicago, trees have been estimated to sequester 5575 metric tons of air pollution, and 315,800 metric tons of C per year at an average rate of 17 metric tons ha⁻¹ y⁻¹ (McPherson et al. 1997). In the Mediterranean climate of Oakland, California, trees sequester 11 metric tons of C ha⁻¹ y⁻¹ (Nowak 1993). In contrast to urban forests, natural forests on average sequester 55 metric tons ha⁻¹ y⁻¹ (Zipperer et al. 1997). The capacity of trees to filter particulates from urban air is based on leaf size and surface roughness (Agrawal 1998).

Urban areas also concentrate materials from elsewhere. For example, the elevation of the surface in old cities is generally higher than the surrounding areas as a result of importing construction materials (Sukopp 1998). A carbon dioxide dome accumulates over cities in association with combustion of fossil fuels (Brazel et al. 2000). Anthropogenically produced forms of N are concentrated in (Lovett et al. 2000) and downwind of cities (Chamiedes et al. 1994). Nitrogen accumulated from human metabolism and fertilizers concentrates downstream of cities. Hence, population density of the watersheds is statistically correlated with N loading in the major rivers of the world (Caraco & Cole 1999).

A useful way to quantify the dependence of urban systems on ecosystems beyond their borders is the concept of the ecological footprint. The ecological footprint of an urban area indexes the amount of land required to produce the material and energetic resources required by, and to process the wastes generated by, a metropolis (Rees 1996). The city of Vancouver, Canada, requires 180 times more land to generate and process materials than the city actually occupies. The concept is highly metaphorical, because the actual networks from which any particular city draws resources, and the areas affected by its waste, may extend around the globe. An analysis of the growth of Chicago (Cronon 1991) showed that a network of resource acquisition extended throughout the western regions of the United States in the late nineteenth century. The metropolis in the postindustrial, information age in nations enjoying a high fossil fuel subsidy has different connections with the hinterland than did the industrially and agriculturally anchored Chicago of a century ago (Bradley 1995). Telecommuting, materially and energetically subsidized recreation, and the alteration of land values for urban uses in the countryside represent a footprint based on urban capital.

ECOSYSTEM PATTERN AND PROCESS There are three ways in which contemporary studies of ecology of cities, or more properly entire metropolitan areas, are prepared to move beyond the classical ecological approaches and to support integration with social and physical sciences. 1. The contemporary assumptions of ecosystem

function are more inclusive than the classical assumptions. 2. The net effects approach to ecosystem budgets has evolved to consider multiple processes and spatial heterogeneity. Finally, 3. the narrow theories that were used to bridge disciplines in the past have been broadened or replaced.

The first tool for integration is the contrast between contemporary and classical assumptions about ecosystem function. Classically, ecologists based studies of urban areas on the assumptions that ecosystems were materially closed and homeostatic systems. Such assumptions were a part of the ecosystem theory used by many early geographers (Zimmerer 1994). These assumptions have been replaced (Zimmerer 1994, Pickett et al. 1992). Consequently, there is a new theory of ecosystems that was not available to those who pioneered the budgetary approach to urban systems (e.g., Boyden et al. 1981). What remains is the basic concept of the ecosystem as a dynamic, connected, and open system (Likens 1992), which can serve the various disciplines (Rebele 1994) that need to be integrated to form a more comprehensive theory to support joint ecological, social, and physical study of urban systems.

Contemporary ecology propounds a systems view that builds on the rigorous budgetary approach to ecosystems (e.g., Jones & Lawton 1995). Of course ecologists necessarily continue to exploit the laws of conservation of matter and energy to generate budgets for ecosystem processes. However, many contemporary studies of ecosystem budgets do not treat systems as though they were black boxes. Rather, the structural details and richness of processes that take place within the boundaries of the system are a major concern of contemporary ecosystem analysis. Contemporary ecosystem ecology exposes the roles of specific species and interactions within communities, flows between patches, and the basis of contemporary processes in historical contingencies. These insights have not been fully exploited in urban ecological studies.

The third feature of contemporary ecology is the breadth of key theories that can be used in integration. Classical ecological theory provided social scientists with only a narrow structure for integration with ecology. The social scientists of the Chicago School, which was active in the early decades of the twentieth century, used ecologically motivated theories of succession and competition, for example. At the time, only the relatively general, deterministic, and equilibrium versions of those theories were available. Contemporary theories of interaction account for both positive and competitive effects, and predictions are based on the actual mechanisms for interaction rather than net effects. In contemporary succession theory, mechanisms other than facilitation are included, and the sequence of communities may not be linear or fixed. In addition, ecologists have come to recognize that those theories have hierarchical structure, which allows them to address different levels of generality and mechanistic detail depending on the scale of the study or the scope of the research questions (Pickett et al. 1994). Hence, social scientists and ecologists now can select the most appropriate levels of generality in a theoretical area for integration. No longer must integration rely on general theories of net effects of such processes as competition and succession.

URBAN ECOLOGY AS A PLANNING APPROACH

Although the first volume of the journal *Ecology* contained a scientific paper devoted to the effect of weather on the spread of pneumonia in New York and Boston (Huntington 1920), the interactions of humans with the urban environment have been primarily the province of planners and landscape architects. For example, Central Park in New York City and other urban parks designed by Frederick Law Olmsted seem intuitively to link environmental properties to human well being in cities. In particular, Olmsted's design for the Boston Fens and Riverway shows ecological prescience in its sophisticated combination of wastewater management and recreational amenity (Spirn 1998). Ian McHarg's (1969) *Design with Nature* alerted planners and architects to the value of incorporating knowledge of ecological and natural features among the usual engineering, economic, and social criteria when developing a regional plan. In McHarg's approach, environmental risks and amenities of different types are mapped on separate layers. The composite map suggests where certain types of development should or should not occur. This approach presaged the technology of Geographic Information Systems (GIS), which has become an important tool to incorporate multiple criteria in planning (Schlutnik 1992, Grove 1997) such as those proposed by McHarg (1969). A more explicit ecological approach is that of Spirn (1984), who examined how natural processes are embedded in cities, and how the interaction between the built environment and natural processes affected economy, health, and human community. For instance, she showed how the forgotten environmental template of drainage networks continued to affect infrastructure and the social structure of a Philadelphia neighborhood.

The planning perspective of human ecology is especially strong in Europe (Sukopp 1998). Planning in Germany has been heavily influenced by a national program of biotope mapping that includes cities (Sukopp 1990, Werner 1999). This program includes descriptions of the flora and fauna of biotopes as a key to identifying types of habitats that are significant for 1. protecting natural resources, 2. quality of life, and 3. a sense of place and identity in the city (Werner 1999). In addition to identifying specific biotopes, researchers in Mainz have mapped the distribution of flora and fauna, natural phenomena, and recreational activities within the biotopes (Frey 1998). Similar research by the Polish Academy of Sciences has focused on urban and suburban areas. The research included studies of soils and abiotic ecosystem components, and research by social scientists in a mosaic of habitats with different degrees of development (Zimny 1990). Building upon the foundation of vegetation classification in cities, Brady et al. (1979) proposed a continuum of habitats from the natural to the highly artificial. Dorney (1977), using a similar approach, proposed an urban-rural continuum from a planning perspective and identified six representative land zones—central business district, old subdivisions, new subdivisions, urban construction zones, urban fringe, and rural. Each zone was characterized by three components or subsystems: cultural history,

abiotic characteristics, and biotic features. We review the status and implication of such integrated classifications later.

Urban ecology manifest as city planning is contrasted with spatial planning (de Boer & Dijkstra 1998) in which primary motivations are the degree of segregation or aggregation of different economic and social functions, efficiency of transportation and delivery of utilities, and efficient filling of undeveloped space. Additional components of urban planning said to have ecological foundations include life cycle analysis of products, utility planning based on use rather than medium, efficiency of resource use, exploitation of green infrastructure, and requirements for monitoring of the results (Breuste et al. 1998).

Although the planning described above is ecologically motivated, and it relies on mapping to describe environmental amenities, it is rarely based on data concerning ecological function. It therefore relies on general ecological principles and assumptions, and on the success of prior case histories (Flores et al. 1997). The insights of urban ecology as planning are summarized in manuals and codified in zoning and planning practice. However, like other environmental practices, these insights may not be applicable in novel ecological circumstances. Given the changing forms of cities in both Europe and the United States, novel ecological circumstances may be in the offing.

AN INTEGRATED FRAMEWORK FOR URBAN ECOLOGICAL STUDIES

We see three opportunities for improving the theory to understand urban systems. First, rather than modeling human systems and biogeophysical systems separately, understanding will be improved by using integrated frameworks that deal with social and biogeophysical processes on an equal footing (Groffman & Likens 1994). Second, knowing that the spatial structure of biogeochemical systems can be significant for their function (Pickett et al. 2000), we hypothesize that the spatial heterogeneity so obvious in urban systems also has ecological significance (Figure 1). Third, insights from hierarchy theory can organize both the spatial models of urban systems and the structure of the integrated theory developed to comprehend them. We explore and combine these themes below.

Social Ecology and Social Differentiation

The study of social structures, and how those structures come to exist, are the key social phenomena to support integrated study of the ecology of urban systems. It is increasingly difficult to determine where biological ecology ends and social ecology begins (Golley 1993). Indeed, the distinction between the two has diminished through the convergence of related concepts, theories, and methods in the biological, behavioral, and social sciences. Social ecology is a life science focusing

on the ecology of various social species such as ants, wolves, or orangutans. We may also study *Homo sapiens* as an individual social species or comparatively with the ecology of other social species. The subject matter of social ecology, like that of biological ecology, is stochastic, historic, and hierarchical (Grove & Burch 1997). In other words, living systems are not deterministic; they exhibit historical contingencies that cannot be predicted from physical laws alone (Botkin 1990, Pickett et al. 1994).

The underlying basis for this life science approach to the study of human ecological systems depends upon three points (Grove & Burch 1997):

1. *Homo sapiens*, like all other species, are not exempt from physical, chemical, or biological processes. Biophysical and social characteristics of humans are shaped by evolution and, at the same time, shape the environment in which *Homo sapiens* live;
2. *Homo sapiens*, like some other species, exhibit social behavior and culture; and
3. Social and cultural traits are involved fundamentally in the adaptation of social species to environmental conditions.

Human ecology must reconcile social and biological facts to understand the behavior of *Homo sapiens* over time (Machlis et al. 1997). Such a biosocial approach to human ecological systems (Burch 1988, Field & Burch 1988, Machlis et al. 1997) stands in contrast to a more traditional geographic or social approach (see Hawley 1950, Catton 1994). This is not to say that social sciences such as psychology, geography, anthropology, sociology, economics, and political science are not important to social ecology. They are, because the most fundamental trait that distinguishes humans and their evolutionary history from other species—both social and nonsocial—is that human social development has enabled the species to escape local ecosystem limitations so that local ecosystems no longer regulate human population size, structure, or genetic diversity (Diamond 1997). Nowhere is this more apparent than in urban ecosystems.

One of the major tools for integration between social and biogeophysical sciences is in the phenomenon of social differentiation. All social species are characterized by patterns and processes of social differentiation (van den Berghe 1975). In the case of humans, social differentiation or social morphology has been a central focus of sociology since its inception (Grusky 1994). In particular, social scientists have used concepts of social identity (i.e., age, gender, class, caste, and clan) and social hierarchies to study how and why human societies become differentiated (Burch & DeLuca 1984, Machlis et al. 1997).

Social differentiation is important for human ecological systems because it affects the allocation of critical resources, including natural, socioeconomic, and cultural resources. In essence, social differentiation determines “who gets what, when, how and why” (Lenski 1966, Parker & Burch 1992). Being rarely equitable, this allocation of critical resources results in rank hierarchies. Unequal access to and control over critical resources is a consistent fact within and between households,

communities, regions, nations, and societies (Machlis et al. 1997). Five types of sociocultural hierarchies are critical to patterns and processes of human ecological systems: wealth, power, status, knowledge, and territory (Burch & DeLuca 1984). Wealth is access to and control over material resources in the form of natural resources, capital, or credit. Power is the ability to alter others' behavior through explicit or implicit coercion (Wrong 1988). The powerful have access to resources that are denied the powerless. One example is politicians who make land-use decisions or provide services for specific constituents at the expense of others. Status is access to honor and prestige and the relative position of an individual (or group) in an informal hierarchy of social worth (Lenski 1966). Status is distributed unequally, even within small communities, but high-status individuals may not necessarily have access to either wealth or power. For instance, a minister or an imam may be respected and influential in a community even though he or she is neither wealthy nor has the ability to coerce other people's behavior. Knowledge is access to or control over specialized types of information, such as technical, scientific, and religious. Not everyone within a social system has equal access to all types of information. Knowledge often provides advantages in terms of access to and control over the critical resources and services of social institutions. Finally, territory is access to and control over critical resources through formal and informal property rights (Burch et al. 1972, Bromley 1991).

Social differentiation of human ecological systems has a spatial dimension characterized by patterns of territoriality and heterogeneity (Morrill 1974, Burch 1988). As Burch (1988) noted, "Intimate and distant social relations, high and low social classes, favored and despised ethnic, occupational, and caste groupings all have assigned and clearly regulated measures as to when and where those relations should and should not occur." When ecosystem and landscape approaches are combined, the research changes from a question of "who gets what, when, how and why?" to a question of "who gets what, when, how, why and where?" and, subsequently, what are the reciprocal relationships between spatial patterns and sociocultural and biophysical patterns and processes of a given area (Grove 1997)?

Various processes of social differentiation occur at different scales and have corresponding spatial patterns and biophysical effects (Grove & Hohmann 1992). Based on existing social and ecological theory, examples include global and regional urban-rural hierarchies (Morrill 1974), the distribution of land uses within urban areas (Guest 1977), the stratification of communities within residential land uses (Logan & Molotch 1987), and the social differentiation of ownerships and households within communities (Burch & Grove 1993, Grove 1995).

Spatial Heterogeneity

A human landscape approach may be understood as the study of the reciprocal relationships between patterns of spatial heterogeneity and sociocultural and biophysical processes. Further, when human ecosystem and landscape approaches are combined, human ecosystem types are defined as homogeneous areas for a

specified set of sociocultural and biophysical variables within a landscape. Analyses then focus on two primary issues: 1. the development and dynamics of spatial heterogeneity, and 2. the influences of spatial patterns on cycles and fluxes of critical ecosystem resources (e.g., energy, materials, nutrients, genetic and non-genetic information, population, labor, capital, organizations, beliefs, or myths). For instance, the development and dynamics of heterogeneity in a watershed spanning urban to rural conditions may influence and be influenced by sociocultural and biophysical processes. Patches within the watershed may function as either sources or sinks as well as to regulate flows and cycles of critical resources between other patches. The delineation and classification of these relatively homogeneous patches is based on a limited number of representative sociocultural and biophysical indicators (Burch & DeLuca 1984, Parker & Burch 1992), and the patches are studied as black boxes with fluxes and cycles of critical resources between areas (Zonneveld 1989). The spatial linkages between the social and ecological differentiation of the watershed and the relationship of the linkages to different types of allocation mechanisms at different scales are important for understanding the flows and cycles of critical resources within the watershed.

Hydrologists have recognized mosaics of spatial heterogeneity in the variable source area (VSA) approach. They examine how the abiotic attributes of different patches within a watershed—such as temperature and physical characteristics including topography, soil properties, water table depth, and antecedent soil moisture—contribute variable amounts of water and nutrients to streamflow, depending upon their spatial location in the watershed (Black 1991). This VSA approach can be integrated with a delineation of patches based upon the biotic attributes of the watershed, such as vegetation structure and species composition (Bormann & Likens 1979), and the social attributes of the watershed, such as indirect effects from land-use change and forest/vegetation management, and direct effects from inputs of fertilizers, pesticides, and toxins, to examine how the abiotic, biotic, and social attributes of different patches within a watershed contribute variable amounts of water and nutrients to streamflow, depending upon their spatial location in the watershed (Grove 1996). This integrated VSA approach combines nested hierarchies of land use and land cover, sociopolitical structures, and watershed heterogeneity (Figure 2). GIS is a useful tool for analyzing nested hierarchies of spatial heterogeneity.

VSA approaches can be linked to additional social processes. For example, catchments can be examined via hydrological, land-use, and economic models (Costanza et al. 1990). The three components can be combined into an ecosystem model composed of grid cells within a catchment. The integrated model is built up from a basic model that has hydrologic and ecologic components, but no economic components. Therefore, in the basic model, human behavior causing land-use change must be considered as a factor external to the focal catchment. To construct truly integrated ecological-economic models, major nutrient, water, productivity, and successional components of the basic model must be combined with land-use and economic valuations (Bockstael et al. 1994). The integrated model calculates

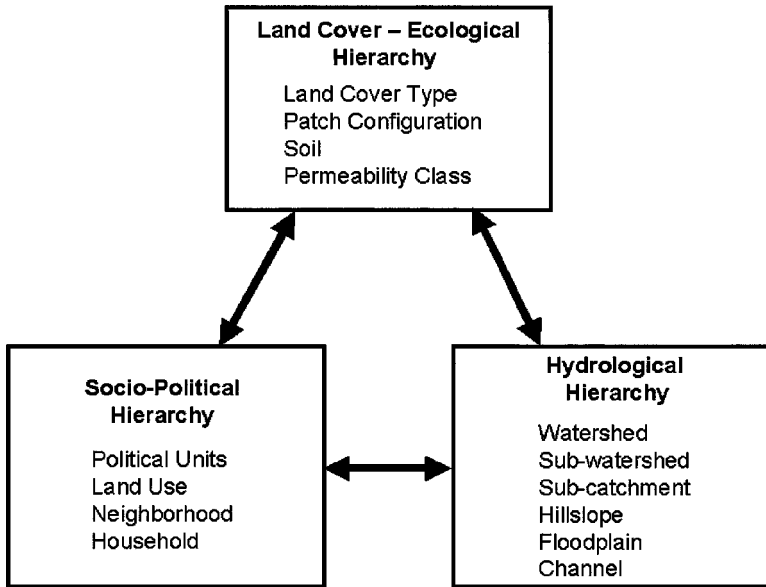


Figure 2 Three interacting nested hierarchies of spatial heterogeneity representing key disciplinary perspectives used in modeling watershed function in urban areas. Land cover represents nested ecological structures that control interception and runoff. The sociopolitical hierarchy contains nested units of environmental decision making and resource use. The hydrological hierarchy indicates the nesting of spatially differentiated units connected by runoff and runoff dynamics.

land-use designation through a habitat-switching module that determines when, through natural succession or weather-driven ecological catastrophe (e.g., floods), the habitat shifts from one type to another. Hypothetical human-caused land-use changes can be imposed exogenously using the integrated model. Recognizing that the ecological effects of human activity are driven by the choices people make concerning stocks of natural capital, the economic modeling uses an understanding of how land-use decisions are made by individuals and how they are based on both the ecological and economic features of the landscape. Again, GIS serves as a tool for manipulating the spatial data on which the model depends, and for assessing the model output over space.

The Human Ecosystem Framework and Urban Ecological Systems

An integrated framework for analyzing urban systems as social, biological, and physical complexes now emerges. Social scientists have focused on interactions between humans and their environments since the self-conscious origins of their

disciplines. However, the explicit incorporation of the ecosystem concept within the social sciences dates to Duncan's (1961, 1964) articles "From Social System to Ecosystem" and "Social Organization and the Ecosystem." Recently, the social sciences have focused increasingly on the ecosystem concept because it has been proposed and used as an organizing approach for natural resource policy and management (Rebele 1994).

The ecosystem concept and its application to humans is particularly important because of its utility as a framework for integrating the physical, biological, and social sciences. The ecosystem concept owes its origin to Tansley (1935), who noted that ecosystems can be of any size, as long as the concern is with the interaction of organisms and their environment in a specified area. Further, the boundaries of an ecosystem are drawn to answer a particular question. Thus, there is no set scale or way to bound an ecosystem. Rather, the choice of scale and boundary for defining any ecosystem depends upon the question asked and is the choice of the investigator. In addition, each investigator may place more or less emphasis on the chemical transformations and pools of materials drawn on or created by organisms; or on the flow, assimilation, and dissipation of biologically metabolizable energy; or on the role of individual species or groups of species on flows and stocks of energy and matter. The fact that there is so much choice in the scales and boundaries of ecosystems, and how to study and relate the processes within them, indicates the profound degree to which the ecosystem represents a research approach rather than a fixed scale or type of analysis.

Although the ecosystem concept is flexible enough to account for humans and their institutions (Tansley 1935, Rebele 1994), the application of an ecosystem approach to the study of human ecosystems requires additional analytical components. The analytical framework (Figure 3) we use here (see Burch & DeLuca 1984, Machlis et al. 1997, Pickett et al. 1997) is not itself a theory. As Machlis et al. (1997: p. 23) noted,

"This human ecosystem model is neither an oversimplification nor caricature of the complexity underlying all types of human ecosystems in the world. Parts of the model are orthodox to specific disciplines and not new. Other portions of the model are less commonplace—myths as a cultural resource, justice as a critical institution. Yet we believe that this model is a reasonably coherent whole and a useful organizing concept for the study of human ecosystems as a life science."

Several elements are critical to the successful application of this framework. First, it is important to recognize that the primary drivers of human ecosystem dynamics are both biophysical and social. Second, there is no single determining driver of anthropogenic ecosystems. Third, the relative significance of drivers may vary over time. Fourth, components of this framework need to be examined simultaneously in relationship to each other (Machlis et al. 1997). Finally, researchers need to examine how dynamic biological and social allocation mechanisms such as ecological constraints, economic exchange, authority, tradition, and knowledge affect the distribution of critical resources including energy, materials, nutrients,

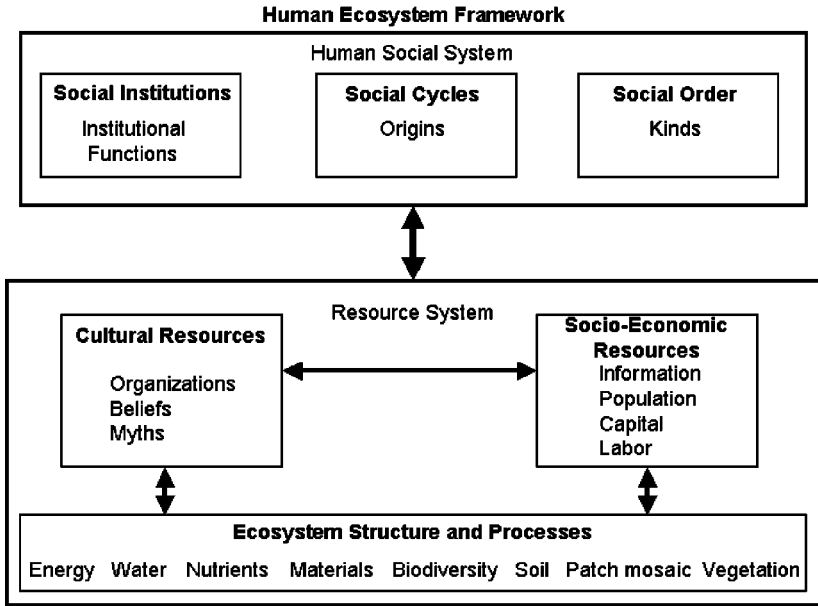


Figure 3 A human ecosystem framework for integrating biogeophysical and social structures and processes. This conceptual structure shows the most general components of any ecosystem that includes or is affected by humans. The nesting of the boxes indicates the inclusion of specific structures or processes within more general phenomena. The social system contains social institutions which function for provision of government, administration of justice, delivery of health services, provision of sustenance, etc. Social order is determined by factors of individual and group identity, formal and informal norms of behavior, and hierarchies that determine allocation of resources. The resource system is founded on biocological structures and processes that include the standard subjects of ecology texts. The resource system also includes cultural and socioeconomic resources, which interact with biocological resources in determining the dynamics of the social system. Based loosely on the work of Machlis et al. (1997). Further ecological details added by Pickett et al. (1997).

population, genetic and nongenetic information, labor, capital, organizations, beliefs, and myths within any human ecosystem (Parker & Burch 1992).

CONCLUSIONS

Although there is a wealth of information on the terrestrial components of urban ecological systems, much of it is organized from the perspective of ecology in cities. This perspective stands in contrast to a more comprehensive perspective identified as the ecology of cities (Grimm et al. 2000). Studies of ecology in cities

have exposed the environmental stresses, subsidies, and constraints that affect urban biota and have documented that the biotic components of metropolitan areas have considerable predictability. In addition, the capacity of certain organisms to adapt to urban environments results in characteristic assemblages.

An alternative approach to urban ecology exists in landscape architecture and planning. This professional practice is motivated by a desire to incorporate ecological principles, to make environmental amenities available to metropolitan residents, and to decrease the negative impacts of urban resource demand and waste on environments elsewhere. Although floristic and faunistic descriptions from urban sites are frequently used in design and planning, there are few data available on ecological functions in cities that can inform such practice. Furthermore, the rapidly changing spatial forms of urban growth and change, and the complex of environmental factors that interact in and around cities, make simple environmental extrapolations risky. Although most of the urban ecological research that has been motivated by planning is of the sort that can be labeled ecology in cities, the field often takes a more comprehensive approach that expresses the ideal of ecology of cities.

In basic ecological research the ecology of the city was first addressed by budgetary studies. Classically this approach has been informed by a biogeochemical perspective based on closed, homeostatic systems. Material and energy budgets of urban systems have been estimated under this rubric. Of course the budgetary approach works whether systems are closed or not, or externally regulated or not. However, assumptions about spatial uniformity and that social agents are external to the ecological processes are questionable.

The distinct ecological approaches classically applied to urban research, and the parallel planning approach, point to the need for integration of different disciplinary perspectives. We have presented a framework that uses middle level theories from ecology and social sciences to identify key factors that should govern the structure and function of biotic, abiotic, and socioeconomic processes in and around cities. This framework is identified as a human ecosystem model, in which both social and ecological processes are integral. Furthermore, the spatial heterogeneity in the biogeophysical and social components of urban systems can be portrayed as patch dynamics. Because patch dynamics can be addressed over many nested scales, structure-function relationships in the human ecosystem can be examined from household to region. The integrative tools and existing data prepare urban ecological studies to continue to benefit from the nature in cities approach, as well as to exploit the contemporary concerns of ecology with spatially heterogeneous, adaptive, self-organizing networks of entire metropolitan systems.

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LITERATURE CITED

- Adamczewska-Andrzejewska K, Mackin-Rogalska R, Nabaglo L. 1988. The effect of urbanization on density and population structure of *Apodemus agrarius* (Pallas, 1771). *Pol. Ecol. Stud.* 14:171–95
- Adams LW, Leedy DL, eds. 1987. *Integrating Man and Nature in the Metropolitan Environment*. Columbia, MD: Natl. Inst. Urban Wildl.
- Adams LW, Leedy DL, eds. 1991. *Wildlife Conservation in Metropolitan Environments*. Columbia, MD: Natl. Inst. Urban Wildl.
- Adams LW, VanDruff LW. 1998. Introduction. *Urban Ecosyst.* 2:3
- Agrawal M. 1998. Relative susceptibility of plants in a dry tropical urban environment. See Breuste et al. 1998, pp. 603–7
- Airola TM, Buchholz K. 1984. Species structure and soil characteristics of five urban sites along the New Jersey Palisades. *Urban Ecol.* 8:149–64
- Alverson WS, Waller DM, Solheim SL. 1988. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2:348–58
- Andrzejewski R, Babinska-Werka J, Gliwicz J, Goszczynski J. 1978. Synurbization processes in population of *Apodemus agrarius*. I. Characteristics of populations in an urbanization gradient. *Acta Theriol.* 23:341–58
- Bagnall RG. 1979. A study of human impact on an urban forest remnant: Redwood Bush, Tawa, near Wellington, New Zealand. *N. Z. J. Bot.* 17:117–26
- Ballach H-J, Govert J, Kohlmann S, Wittig R. 1998. Comparative studies on the size of annual rings, leaf growth and structure of treetops of urban trees in Frankfurt/Main. See Breuste et al. 1998, pp. 699–701
- Bergen F, Schwerk A, Abs M. 1998. Long-term observation of the fauna of two man-made nature habitats in cities of the Ruhr-Valley area. See Breuste et al. 1998, pp. 618–22
- Bishop JA, Cook LM. 1980. Industrial melanism and the urban environment. *Adv. Ecol. Res.* 11:373–404
- Black PE. 1991. *Watershed Hydrology*. Englewood Cliffs, NJ: Prentice Hall
- Bockstael N, Costanza R, Strand I, Boynton W, Bell K, Wainger L. 1995. Ecological economic modeling and valuation of ecosystems. *Ecol. Econ.* 14:143–59
- Bormann FH, Likens GE. 1979. *Pattern and Process in a Forested Ecosystem*. New York: Springer-Verlag
- Botkin DB. 1990. *Discordant Harmonies: a New Ecology for the Twenty-first Century*. New York: Oxford Univ. Press
- Botkin DB, Beveridge CE. 1997. Cities as environments. *Urban Ecosyst.* 1:3–19
- Bowers MA. 1997. Influence of deer and other factors on an old-field plant community. In *The Science of Overabundance: Deer Ecology and Population Management*, ed. WJ McShea, BH Underwood, JH Rappole, pp. 310–26. Washington, DC: Smithsonian. Inst. Press
- Boyden S, Millar S, Newcombe K, O'Neill B. 1981. *The Ecology of a City and its People: the Case of Hong Kong*. Canberra: Aust. Natl. Univ. Press
- Bradley GA, ed. 1995. *Urban Forest Landscapes: Integrating Multidisciplinary Perspectives*. Seattle: Univ. Wash. Press
- Bradshaw AD, McNeilly T. 1981. *Evolution and pollution*. London: Edward Arnold
- Brady RF, Tobias T, Eagles PFJ, Ohner R,

- Micak J et al. 1979. A typology for the urban ecosystem and its relationship to larger biogeographical landuse units. *Urban Ecol.* 4:11–28
- Brazel A, Selover N, Vose R, Heisler G. 2000. The tale of two cities—Baltimore and Phoenix urban LTER sites. *Climate Res.* 15:123–35
- Breuste J, Feldman H, Uhlmann O, eds. 1998. *Urban Ecology*. Berlin: Springer-Verlag
- Bromley DW. 1991. *Environment and Economy: Property Rights and Public Policy*. Cornwall, UK: TJ
- Brooks RT, Rowntree RA. 1984. Forest area characteristics for metropolitan and non-metropolitan counties of three northeastern states of the United States. *Urban Ecol.* 8:341–46
- Bullock P, Gregory PJ. 1991. Soils: a neglected resource in urban areas. In *Soils in the Urban Environment*, ed. P Bullock, PJ Gregory, pp. 1–5. Oxford, UK: Blackwell Sci.
- Burch WR Jr. 1988. Human ecology and environmental management. In *Ecosystem Management for Parks and Wilderness*, ed. JK Agee, J Darryll, pp. 145–59. Seattle: Univ. Wash. Press
- Burch WR Jr, Cheek NH Jr, Taylor L, eds. 1972. *Social Behavior, Natural Resources, and the Environment*. New York: Harper & Row
- Burch WR Jr, DeLuca D. 1984. *Measuring the Social Impact of Natural Resource Policies*. Albuquerque: Univ. New Mexico Press
- Burch WR Jr, Grove JM. 1993. People, trees, and participation on the urban frontier. *Unasylva* 44:19–27
- Caraco NF, Cole JJ. 1999. Human impact on nitrate export: an analysis using major world rivers. *Ambio* 28:167–70
- Carreiro MM, Howe K, Parkhurst DF, Pouyat RV. 1999. Variations in quality and decomposability of red oak litter along an urban-rural land use gradient. *Biol. Fert. Soils* 30: 258–68
- Catton WR Jr. 1994. Foundation of human ecology. *Sociol. Perspect.* 37:75–95
- Chameides WL, Kasibhatla PS, Yienger J, Levy H. 1994. Growth of continental-scale metro-agro-plexes, regional ozone pollution, and world food production. *Science* 264:74–77
- Churcher PB, Lawton JH. 1987. Predation by domestic cats in an English village. *J. Zool.* 212:439–55
- Collins JP, Kinzig A, Grimm NB, Fagan WF, Hope D et al. 2000. A new urban ecology. *Am. Sci.* 88:416–25
- Costanza R, Sklar FH, White ML. 1990. Modeling coastal landscape dynamics. *BioScience* 40:91–107
- Cronon W. 1991. *Nature's Metropolis: Chicago and the Great West*. New York: Norton
- de Boer J, Dijst M. 1998. Urban development and environmental policy objectives—an outline of a multi-disciplinary research program. See Breuste et al. 1998, pp. 38–42
- Deelstra T. 1998. Towards ecological sustainable cities: strategies, models and tools. See Breuste et al. 1998, pp. 17–22
- De Rudder B, Linke F. 1940. *Biologie der Großstadt*. Dresden: Leipzig
- Diamond JM. 1997. *Guns, Germs, and Steel: the Fate of Human Societies*. New York: Norton
- Dorney RS. 1977. Biophysical and cultural-historic land classification and mapping for Canadian urban and urbanizing landscapes. In *Ecological/biophysical Land Classification in Urban Areas*, ed. Environ. Can., pp. 57–71. Ottawa: Environ. Can.
- Douglas I. 1983. *The Urban Environment*. Baltimore, MD: Edward Arnold
- Dow CL, DeWalle DR. 2000. Trends in evapotranspiration and Bowen ration on urbanizing watersheds in eastern United States. *Water Resour. Res.* 7:1835–43.
- Drayton B, Primack RB. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. *Conserv. Biol.* 10:30–39
- Duncan OD. 1961. From social system to ecosystem. *Sociol. Inq.* 31:140–49
- Duncan OD. 1964. Social organization and the ecosystem. In *Handbook of Modern*

- Sociology*, ed. REL Faris, pp. 37–82. Chicago: Rand McNally
- Effland WR, Pouyat RV. 1997. The genesis, classification, and mapping of soils in urban areas. *Urban Ecosyst.* 1:217–28
- Field DR, Burch WR Jr. 1988. *Rural Sociology and the Environment*. Middleton, WI: Soc. Ecol.
- Flores A, Pickett STA, Zipperer WC, Pouyat RV, Pirani R. 1997. Adopting a modern ecological view of the metropolitan landscape: the case of a greenspace system for the New York City region. *Landsc. Urban Plan.* 39:295–308
- Frey J. 1998. Comprehensive biotope mapping in the city of Mainz—a tool for integrated nature conservation and sustainable urban planning. See Breuste et al. 1998, pp. 641–47
- Garreau J. 1991. *Edge City: Life on the New Frontier*. New York: Doubleday
- Gilbert OL. 1989. *The Ecology of Urban Habitats*. New York/London: Chapman & Hall
- Goldman MB, Groffman PM, Pouyat RV, McDonnell MJ, Pickett STA. 1995. CH₄ uptake and N availability in forest soils along an urban to rural gradient. *Soil Biol. Biochem.* 27:281–86
- Golley FB. 1993. *A History of the Ecosystem Concept in Ecology: More than the Sum of the Parts*. New Haven: Yale Univ. Press
- Greenwood EF, ed. 1999. *Ecology and Landscape Development: a History of the Mersey Basin*. Liverpool: Liverpool Univ. Press
- Grimm NB, Grove JM, Pickett STA, Redman CL. 2000. Integrated approaches to long-term studies of urban ecological systems. *BioScience* 50:571–84
- Groffman PM, Likens GE, eds. 1994. *Integrated Regional Models: Interactions Between Humans and Their Environment*. New York: Chapman & Hall
- Groffman PM, Pouyat RV, McDonnell MJ, Pickett STA, Zipperer WC. 1995. Carbon pools and trace gas fluxes in urban forest soils. In *Soil Management and Greenhouse Effect*, ed. R Lal, J Kimble, E Levine, BA Stewart, pp. 147–58. Boca Raton: CRC Lewis
- Grove JM. 1995. Excuse me, could I speak to the property owner please? *Comm. Prop. Resour. Dig.* 35:7–8
- Grove JM. 1996. *The relationship between patterns and processes of social stratification and vegetation of an urban-rural watershed*. PhD dissertation. Yale Univ., New Haven. pp. 109
- Grove JM. 1997. New tools for exploring theory and methods in human ecosystem and landscape analyses: computer modeling, remote sensing and geographic information systems. In *Integrating Social Sciences and Ecosystem Management*, ed. HK Cordell, JC Bergstrom. Champaign: Sagamore
- Grove JM, Burch WR Jr. 1997. A social ecology approach and application of urban ecosystem and landscape analyses: a case study of Baltimore, Maryland. *Urban Ecosyst.* 1:259–75
- Grove JM, Hohmann M. 1992. GIS and social forestry. *J. For.* 90:10–15
- Grusky DB, ed. 1994. *Social Stratification: Class, Race, and Gender in Sociological Perspective*. Boulder: Westview
- Guest AM. 1977. Residential segregation in urban areas. In *Contemporary Topics in Urban Sociology*, ed. KP Schwirian, pp. 269–336. Morristown: Gen. Learn.
- Guilden JM, Smith JR, Thompson L. 1990. Stand structure of an old-growth upland hardwood forest in Overton Park, Memphis, Tennessee. In *Ecosystem Management: Rare Species and Significant Habitats*, ed. RS Mitchell, CJ Sheviak, DJ Leopold, pp. 61–66. Albany: New York State Mus.
- Haspel C, Calhoun RE. 1991. Ecology and behavior of free-ranging cats in Brooklyn, New York. See Adams & Leedy 1991, pp. 27–30
- Hawley D. 1950. *Human Ecology: A Theory of Community Structure*. New York: Ronald
- Hobbs ER. 1988. Species richness in urban forest patches and implications for urban landscape diversity. *Landsc. Ecol.* 1:141–52
- Hough M. 1995. *Cities and Natural Processes*. London: Routledge
- Huntington E. 1920. The control of pneumonia an influenza by weather. *Ecology* 1:1–23

- Iida S, Nakashizuka T. 1995. Forest fragmentation and its effect on species diversity in suburban coppice forests in Japan. *For. Ecol. Manage.* 73:197–210
- Jones CG, Lawton JH, eds. 1995. *Linking Species and Ecosystems*. New York: Chapman & Hall
- Katz B, Bradley J. 1999. Divided we sprawl. *Atl. Mon.* 284:26–42
- Klausnitzer B, Richter K. 1983. Presence of an urban gradient demonstrated for carabid associations. *Oecologia* 59:79–82
- Klotz S. 1990. Species/area and species/inhabitants relations in European cities. See Sukopp 1990a, pp. 100–12
- Kowarik I. 1990. Some responses of flora and vegetation to urbanization in Central Europe. See Sukopp 1990a, pp. 45–74
- Lawrence HW. 1995. Changing forms and persistent values: historical perspectives on the urban forest. See Bradley 1995, pp. 17–40
- Lenski GE. 1966. *Power and Privilege: a Theory of Social Stratification*. New York: McGraw-Hill
- Likens GE. 1992. *Excellence in Ecology, Vol. 3. The Ecosystem Approach: Its Use and Abuse*. Oldendorf/Luhe: Ecol. Inst.
- Logan JR, Molotch HL. 1987. *Urban Fortunes: the Political Economy of Place*. Berkeley: Univ. Calif. Press
- Lovett GM, Traynor MM, Pouyat RV, Carreiro MM, Zhu W, Baxter J. 2000. Nitrogen deposition along an urban-rural gradient in the New York City metropolitan area. *Environ. Sci. Technol.* 34:4294–300
- Luniak M, Pisanski B. 1994. State of research into the fauna of Warsaw (up to 1990). *Mem. Zool.* 49:155–65
- Machlis GE, Force JE, Burch WR Jr. 1997. The human ecosystem part I: the human ecosystem as an organizing concept in ecosystem management. *Soc. Nat. Res.* 10:347–67
- Mackin-Rogalska R, Pinowski J, Solon J, Wojcik Z. 1988. Changes in vegetation, avifauna, and small mammals in a suburban habitat. *Pol. Ecol. Stud.* 14:239–330
- Makse HA, Havlin S, Stanley HE. 1995. Modelling urban growth patterns. *Nature* 377: 608–12
- Matlack GR. 1997. Land use and forest habitat distribution in the hinterland of a large city. *J. Biogeogr.* 24:297–307
- Matthews MJ, O'Connor S, Cole RS. 1988. Database for the New York State urban wildlife habitat inventory. *Landsc. Urban Plan.* 15:23–37
- McDonnell MJ, Pickett STA, eds. 1993. *Humans as Components of Ecosystems: the Ecology of Subtle Human Effects and Populated Areas*. New York: Springer-Verlag
- McDonnell MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV et al. 1997. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosyst.* 1:21–36
- McDonnell MJ, Pickett STA, Pouyat RV. 1993. The application of the ecological gradient paradigm to the study of urban effects. See McDonnell & Pickett 1993, pp. 175–89
- McHarg I. 1969. *Design with Nature*. Garden City, NJ: Doubleday/Nat. Hist.
- McPherson EG, Nowak D, Heisler G, Grimmond S, Souch C et al. 1997. Quantifying urban forest structure, function, and value: the Chicago urban forest climate project. *Urban Ecosyst.* 1:49–61
- Medley KE, McDonnell MJ, Pickett STA. 1995. Human influences on forest- landscape structure along an urban-to-rural gradient. *Prof. Geogr.* 47:159–68
- Moran MA. 1984. Influence of adjacent land use on understory vegetation of New York forests. *Urban Ecol.* 8:329–40
- Morrill RL. 1974. *The Spatial Organization of Society*. Duxbury, MA: Duxbury
- Mucina L. 1990. Urban vegetation research in European COMECON countries and Yugoslavia: a review. See Sukopp 1990a, pp. 23–43
- Nilon CH, Pais RC. 1997. Terrestrial vertebrates in urban ecosystems: developing hypotheses for the Gwynns Falls Watershed in Baltimore, Maryland. *Urban Ecosyst.* 1:247–57

- Nowak DJ. 1993. Atmospheric carbon reduction by urban trees. *J. Environ. Manage.* 37:207–17
- Nowak DJ. 1994. Urban forest structure: the state of Chicago's urban forest. In *Chicago's Urban Forest Ecosystem: Results of the Chicago Urban Forest Climate Project*, ed. EG McPherson, D Nowak, RA Rowntree, pp. 140–64. Radnor, PA: USDA Forest Serv.
- Nowak DJ, McBride JR. 1992. Differences in Monterey pine pest populations in urban and natural forests. *For. Ecol. Manage.* 50:133–44
- Nowak DJ, Rowntree R, McPherson EG, Sissini SM, Kerkmann E, Stevens JC. 1996. Measuring and analyzing urban tree cover. *Landsc. Urban Plan.* 36:49–57
- Noyes JH, Progulskes DR. 1974. *Wildlife in an Urbanizing Environment*. Amherst: Mass. Coop. Ext. Serv., Univ. Mass.
- Odum EP. 1997. *Ecology: a Bridge Between Science and Society*. Sunderland, MA: Sinauer
- Odum HT, Odum EC. 1980. *Energy Basis for Man and Nature*. New York: McGraw-Hill
- Oke TR. 1973. City size and urban heat island. *Atmos. Environ.* 7:769–79
- Oke TR. 1995. The heat island of the urban boundary layer: characteristics, causes and effects. In *Wind Climate in Cities*, ed. JE Cermak, pp. 81–107. Netherlands: Kluwer Acad.
- Parker JK, Burch WR Jr. 1992. Toward a social ecology for agroforestry in Asia. In *Social Science Applications in Asian Agroforestry*, ed. WR Burch Jr, JK Parker, pp. 60–84. New Delhi: IBH
- Paul MJ, Meyer JL. 2001. Riverine ecosystems in an urban landscape. *Annu. Rev. Ecol. Syst.* 32: In press
- Pickett STA, Burch WR Jr, Dalton SD, Foresman TW. 1997. Integrated urban ecosystem research. *Urban Ecosyst.* 1:183–84
- Pickett STA, Cadenasso ML, Jones CG. 2000. Generation of heterogeneity by organisms: creation, maintenance, and transformation. In *Ecological Consequences of Habitat Heterogeneity*, ed. M Hutchings, L John, A Stewart, pp. 33–52. New York: Blackwell
- Pickett STA, Kolasa J, Jones CG. 1994. *Ecological Understanding: The Nature of Theory and the Theory of Nature*. San Diego: Academic
- Pickett STA, Parker VT, Fiedler PL. 1992. The new paradigm in ecology: implications for conservation biology above the species level. In *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management*, ed. PL Fiedler, SK Jain, pp. 65–88. New York: Chapman & Hall
- Pouyat RV, McDonnell MJ. 1991. Heavy metal accumulation in forest soils along an urban to rural gradient in southern NY, USA. *Water Soil Air Pollut.* 57/58:797–807
- Pouyat RV, McDonnell MJ, Pickett STA. 1997. Litter decomposition and nitrogen mineralization along an urban-rural land use gradient. *Urban Ecosyst.* 1:117–31
- Pouyat RV, McDonnell MJ, Pickett STA, Groffman PM, Carreiro MM et al. 1995. Carbon and nitrogen dynamics in oak stands along an urban-rural gradient. In *Carbon Forms and Functions in Forest Soils*, ed. JM Kelly, WW McFee, pp. 569–87. Madison, WI: Soil Sci. Soc. Am.
- Pouyat RV, Parmelee RW, Carreiro MM. 1994. Environmental effects of forest soil-invertebrate and fungal densities in oak stands along an urban-rural land use gradient. *Pedobiologica* 38:385–99
- Rapoport EH. 1993. The process of plant colonization in small settlements and large cities. See McDonnell & Pickett 1993, pp. 190–207
- Rebele F. 1994. Urban ecology and special features of urban ecosystems. *Global Ecol. Biogeogr. Lett.* 4:173–87
- Rees WE. 1996. Revisiting carrying capacity: area-based indicators of sustainability. *Popul. Environ.* 17:195–215
- Rogers GF, Rowntree RA. 1988. Intensive surveys of structure and change in urban natural areas. *Landsc. Urban Plan.* 15:59–78
- Rowntree RA. 1995. Toward ecosystem management: shifts in the core and the context of urban forest ecology. See Bradley 1995, pp. 43–59

- Rudnický JL, McDonnell MJ. 1989. Forty-eight years of canopy change in a hardwood-hemlock forest in New York City. *Bull. Torrey Bot. Club* 116:52–64
- Salisbury EJ. 1943. The flora of bombed areas. *Proc. R. Inst. G. B.* 32:435–55
- Schlutink G. 1992. Integrated remote sensing, spatial information systems, and applied models in resource assessment, economic development, and policy analysis. *Photogramm. Eng. Remote Sens.* 58:1229–37.
- Schmid JA. 1975. *Urban Vegetation: a Review and Chicago Case Study*. Chicago: Univ. Chicago Dep. Geogr.
- Sissini SM, Emmerich A. 1995. Methodologies, results and applications of natural resource assessment in New York City. *Nat. Areas J.* 15:175–88
- Spirn AW. 1984. *The Granite Garden: Urban Nature and Human Design*. New York: Basic Books
- Sprin AW. 1998. *The Language of Landscape*. New Haven: Yale Univ. Press
- Stearns FW. 1971. Urban botany—an essay on survival. *Univ. Wis. Field Stn. Bull.* 4:1–6
- Steinberg DA, Pouyat RV, Parmelee RW, Groffman PM. 1997. Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. *Soil Biol. Biochem.* 29:427–30
- Sukopp H. 1998. Urban ecology—scientific and practical aspects. See Breuste et al. 1998, pp. 3–16
- Sukopp H, ed. 1990a. *Urban Ecology: Plants and Plant Communities in Urban Environments*. The Hague: SPB Acad.
- Sukopp H. 1990b. Urban ecology and its application in Europe. See Sukopp 1990a, pp. 1–22
- Sukopp H, Weiler S. 1988. Biotope mapping and nature conservation strategies in urban areas of the Federal Republic of Germany. *Landsch. Urban Plan.* 15:39–58
- Tansley AG. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307
- United Nations. 1993. *World Population Prospects*. New York: United Nations
- van den Bergh PL. 1975. *Man in Society: a Biosocial View*. New York: Elsevier
- VanDruff LW, Bolen EG, San Julian GJ. 1994. Management of urban wildlife. In *Research and Management Techniques for Wildlife and Habitats*, ed. TA Bookhout, pp. 507–30. Bethesda, MD: Wildl. Soc.
- VanDruff LW, Rowse RN. 1986. Habitat association of mammals in Syracuse, New York. *Urban Ecol.* 9:413–34
- Velguth PH, White DB. 1998. Documentation of genetic differences in a volunteer grass, *Poa annua* (annual meadow grass), under different conditions of golf course turf, and implications for urban landscape plant selection and management. See Breuste et al. 1998, pp. 613–17
- Waggoner PE, Ovington JD, eds. 1962. *Proceedings of the Lockwood Conference on the Suburban Forest and Ecology*. New Haven: Conn. Agric. Exp. Stn.
- Werner P. 1999. Why biotope mapping in populated areas? *Deinsea* 5:9–26
- Wetterer JK. 1997. *Urban Ecology. Encyclopedia of Environmental Sciences*. New York: Chapman & Hall
- White CS, McDonnell MJ. 1988. Nitrogen cycling processes and soil characteristics in an urban versus rural forest. *Biogeochemistry* 5:243–62
- Witt K. 1996. Species/plot turnovers from repeated atlas mapping of breeding birds in southern Berlin 1980 and 1990. *Acta Orn.* 31:81–84
- Wittig R. 1998. Urban development and the integration of nature: reality or fiction? See Breuste et al. 1998, pp. 593–99
- Wrong DH. 1988. *Power: its Forms, Bases, and Uses*. Chicago: Univ. Chicago Press
- Wu L, Antonovics J. 1975a. Zinc and copper uptake by *Agrostis stolonifera* tolerant to zinc and copper. *New Phytol.* 75:231–37
- Wu L, Antonovics J. 1975b. Experimental ecological genetics in *Plantago*. II. Lead tolerance in *Plantago lanceolata* and *Cynodon*

- dactylon* from a roadside. *Ecology* 57:205–8
- Zimmerer KS. 1994. Human geography and the “new ecology:” the prospect and promise of integration. *Ann. Assoc. Am. Geogr.* 84:108–25
- Zimny H. 1990. Ecology of urbanized systems—problems and research in Poland. In *Urban Ecological Studies in Central and Eastern Europe*, ed. M Luniak, pp. 8–18. Warsaw: Pol. Acad. Sci. Inst. Zool.
- Zipperer WC, Foresman TW, Sisinni SM, Pouyat RV. 1997. Urban tree cover: an ecological perspective. *Urban Ecosyst.* 1:229–47
- Zonneveld IS. 1989. The land unit—a fundamental concept in landscape ecology and its applications. *Landsc. Ecol.* 3:67–89



Figure 1 Patchiness in the Rognel Heights neighborhood of Baltimore, Maryland. The spatial heterogeneity of urban systems presents a rich substrate for integrating ecological, socioeconomic, and physical patterns using Geographic Information Systems. The patch mosaic discriminates patches based on the structures of vegetation and the built environment. The base image is a false color infrared orthorectified photo from October 1999. (M.L. Cadenasso, S.T.A Pickett & W.C. Zipperer, unpublished data.)



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