Ecology, 71(4), 1990, pp. 1232–1237

ECOSYSTEM STRUCTURE AND FUNCTION ALONG URBAN–RURAL GRADIENTS: AN UNEXPLOITED OPPORTUNITY FOR ECOLOGY[1]

M. J. McDonnell and S. T. A. Pickett
Institute of Ecosystem Studies, The New York Botanical Garden, Mary Flagler Cary Arboretum, Box AB, Millbrook, New York 12545 USA

Introduction

Urbanization is a massive, unplanned experiment that already affects large acreages and is spreading in many areas of the United States (Alig and Healy 1987). Urban areas are conservatively defined as those with human populations denser than 620 individuals/km^2 (United States Bureau of Census 1980, Bourne and Simmons 1982). In 1989, 74% of the United States population (203 million people) resided in urban areas and that number is expected to increase to >80% by the year 2025 (Fox 1987, Haub and Kent 1989). The increase in urban population throughout the country has resulted in the conversion of cropland, pastures, and forests into urban and suburban environments (Ehrenfeld 1970). Between 1960 and 1970 urban land in the United States increased by 9 million acres, and between 1970 and 1980 it increased by 13 million acres (Frey 1984).

Urbanization can be characterized as an increase in human habitation, coupled with increased per capita energy consumption and extensive modification of the landscape, creating a system that does not depend principally on local natural resources to persist. We can use the term "urbanization" as a convenient shorthand for the ecological forcing functions created by the growth of cities and associated human activities. However, the individual components (e.g., structures, physical and chemical environments, populations, communities, ecosystems, and human culture) must be quantified, and correlations among them assessed, to discover the ecologically important impacts of urban development and change.

The structure of metropolitan areas and their fringes consists of a variety of components, ranging from totally built environments to "natural" or seminatural areas (Mumford 1956, Dickinson 1966, Stearns and Montag 1974; Table 1). Natural areas in an urban context are those not intensively managed by people (e.g., wooded areas in city parks, lakes, ponds, streams, etc.; Andrews and Cranmer-Byng 1981, McDonnell 1988), and often include a high proportion of intentionally and accidentally introduced organisms as well as native species (Gill and Bonnett 1973, Noyes and Proqulske 1974, Numata 1977, Whitney and Adams 1980, Bornkamm et al. 1982, Kunick 1982, Dorney et al. 1984). The ecological study of the effects of urbanization can focus either on metropolitan areas as wholes or on natural areas within metropolitan areas. The study of the metropolis as an ecosystem, including its human inhabitants and institutions, would be a radical expansion of ecology. The study of natural areas along urban–rural gradients is an application of an existing ecological research strategy to a new situation.

This paper indicates how urbanization can be exploited as a research subject in ecology. We indicate how the effects of urbanization can provide a context for answering ecological questions of general importance and applicability, as well as questions that are specific and unique to urbanization. We also introduce a conceptual framework for the ecological study of urbanization.

Urbanization as a Complex Environmental Gradient

The established and successful "gradient paradigm" (Whittaker 1967, Austin 1987, Stevens 1989) provides a useful basis for ecological studies of the spatially varying effects of urbanization (Ter Braak and Prentice 1988). The gradient paradigm can be summarized as the view that environmental variation is ordered in space, and that spatial environmental patterns govern the corresponding structure and function of ecological systems, be they populations, communities, or ecosystems. The degree of the environmental change in space determines, in part, the steepness of the gradient in system structure and function. Of course, interactions within the ecological systems, and between the environmental gradient and the ecological systems will affect the distribution and behavior of systems along the gradient (Terborgh 1971, Roberts 1987).

[1] For reprints of this Special Feature, see footnote 1, page 1231.

TABLE 1. Features of urbanization.

Structural features of urbanization
Dwellings
Factories
Office buildings
Warehouses
Roads
Pipelines
Power lines
Railroads
Channelized waterways
Reservoirs
Sewage disposal facilities
Dumps
Gardens
Parks
Cemeteries
Airports
Biota of urban areas
Crops
Ornamentals
Domestic pets
Pests
Disease organisms
Socio-economic factors

Because urban areas appear so often as a dense, highly developed core, surrounded by irregular rings of diminishing development (Dickinson 1966), the gradient paradigm is a powerful organizing tool for ecological research on urban influences on ecosystems. Like natural environmental gradients, urbanization should present ecologists with a rich spatial array to use in explaining or predicting environmental and ecological effects. Urban–rural gradients, moreover, provide an opportunity to explicitly examine the role of humans.

WHY STUDY ECOLOGICAL SYSTEMS ALONG URBAN–RURAL GRADIENTS?

From an ecologist's perspective, urbanization produces a variety of unprecedented and intense "experimental manipulations." Examples include changes in: (1) disturbance regimes, (2) biota, (3) landscape structure, (4) physiological stresses (e.g., air pollution), and (5) cultural, economic, and political factors. In most cases, both the spatial extent and magnitude of the manipulations are greater than those that ecologists are typically able to produce.

The coarse-scale, anthropogenic manipulations of ecological systems along urban–rural gradients provide an opportunity to address basic questions at various spatial scales. For example, questions related to hierarchy theory could be addressed. The central problem in this theory is to determine at what scale ecological processes and patterns uniquely appear (O'Neill et al. 1986). The relative influences of urban and natural environmental factors on ecosystem patterning, and the extent to which ecosystem processes are also influenced, could be examined most easily along urban–rural gradients, where human influences can be directly quantified.

Likewise, a number of questions that fall within the framework of disturbance theory could be examined. In disturbance theory, manipulations of disturbance regimes are used to determine the significance of different disturbance types, intensities, and frequencies in communities and ecosystems (Pickett and White 1985). The study of the interactions between urbanization and disturbance regimes and their effects on ecological properties provide an excellent opportunity to advance understanding in this general area.

One specific question that could be addressed using changes in disturbance regimes along urban–rural gradients is the balance between autogenesis and allogenesis (Kolasa and Pickett 1990). If various disturbance and stress factors can be attributed to forces either within or outside the community, then the balance of internal and external control of system organization can be contrasted along the gradient.

One additional area of ecological research that could benefit from studies along urban–rural gradients is that of species control on ecosystem fluxes. The simplification of community composition and the introduction of new species in urban areas provides an opportunity to address questions concerning the mechanistic role of species in ecological processes on higher levels of organization.

Finally, the intimate involvement of humans with the urban–rural gradient suggests that it would be an unparalleled situation in which to integrate humans as subjects for ecological study. Human ecology is the discipline that inquires into the patterns and process of interaction of humans with their environments (Boyden 1977, Boyden and Millar 1978, Vayda 1983). Human values, wealth, life-styles, resource use, and waste, etc. must affect and be affected by the physical and biotic environments along urban–rural gradients. The nature of these interactions is a legitimate ecological research topic and one of increasing importance.

Clearly, the interactions among various anthropogenic factors and between anthropogenic and natural variables make urban–rural gradients potentially complex. These interactions must be assessed before analyses such as those suggested above can be carried out. Furthermore, it is certain that urban–rural gradients are not appropriate for all ecological questions. Nevertheless, we believe that such gradients do provide new and sometimes unique opportunites for ecologists to test assumptions and predictions of many ecological theories.

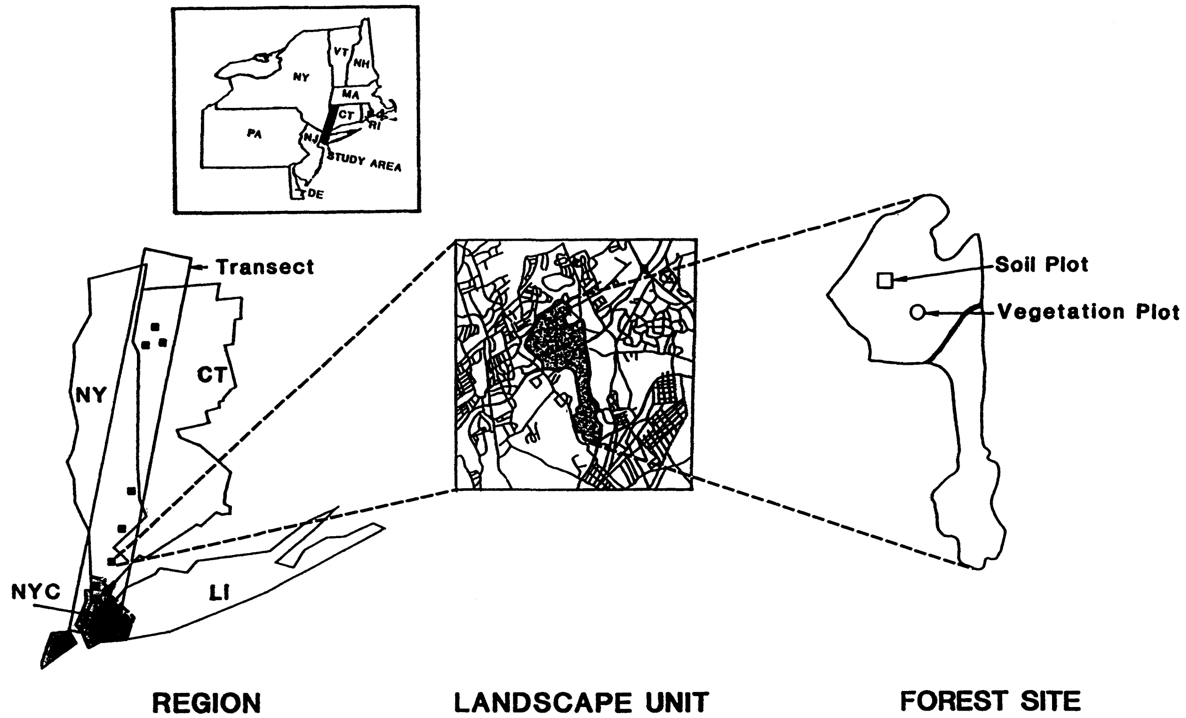

FIG. 1. The various scales involved in the study of ecological systems along urban–rural gradients illustrated by the New York City Metropolitan area. Each scale, ranging from the metropolitan region, through the landscape unit, to the site, can be the focus of ecological study.

SPECIFIC QUESTIONS ALONG THE URBAN–RURAL GRADIENT: AN ILLUSTRATION

We have indicated how the study of ecological systems along urban–rural gradients could be used to address topics of general ecological interest. In this section we will discuss several specific uses of an urban–rural gradient, drawing in part on our study of ecosystems in the New York City Metropolitan area. The region includes a readily measurable gradient of land use radiating from the New York City urban core to suburban and rural areas at increasing distances from the city (Fig. 1). Remnant forest patches still exist in the city as well as elsewhere on the land-use gradient, providing an excellent opportunity to investigate long-term human impacts on forest ecosystems.

Soil resources

A preliminary study of the physical and chemical properties of forest soils along a land-use gradient from New York City to rural Dutchess County revealed that the soils at the urban end of the gradient were more hydrophobic than rural sites (White and McDonnell 1988, *unpublished manuscript*). This novel pattern provides a stimulus to address several ecological questions, including the following: Is the formation of the hydrophobic soil the result of natural processes (Adams et al. 1970, DeBano 1971, Reeder and Jurgensen 1979, McGhie and Posner 1981) or new anthropogenically derived sources? How does the pattern of hydrophobicity vary in time and space? Does it limit resource availability to plants (e.g., by reducing N mineralization)? How does it affect litter decomposition rates and belowground processes? Does it affect gas fluxes from soil to the atmosphere? Is it amplified by other stresses and disturbances? Although these questions are generated by the pattern of contrasting hydrophobicity along the urban–rural gradient, they are relevant to larger concerns of biogeochemical fluxes in a broad range of ecosystems.

Community organization

We know already that forests in highly urban environments differ in both subtle and patent ways from those in the surrounding countryside (Bagnall 1979, Airola and Buchholz 1984, Hobbs 1988, Rudnicky and McDonnell 1989). For instance, urban and suburban forests have a conspicuous proportion of exotic and naturalized species (Bagnall 1979, Airola and Buchholz 1984, Hobbs 1988, Rudnicky and McDonnell 1989), and frequently a lower representation of certain native species. However, little is known about the functional importance of the differences in composition. Likewise, the structure of urban and rural forests differ (Rudnicky and McDonnell 1989). The canopy height

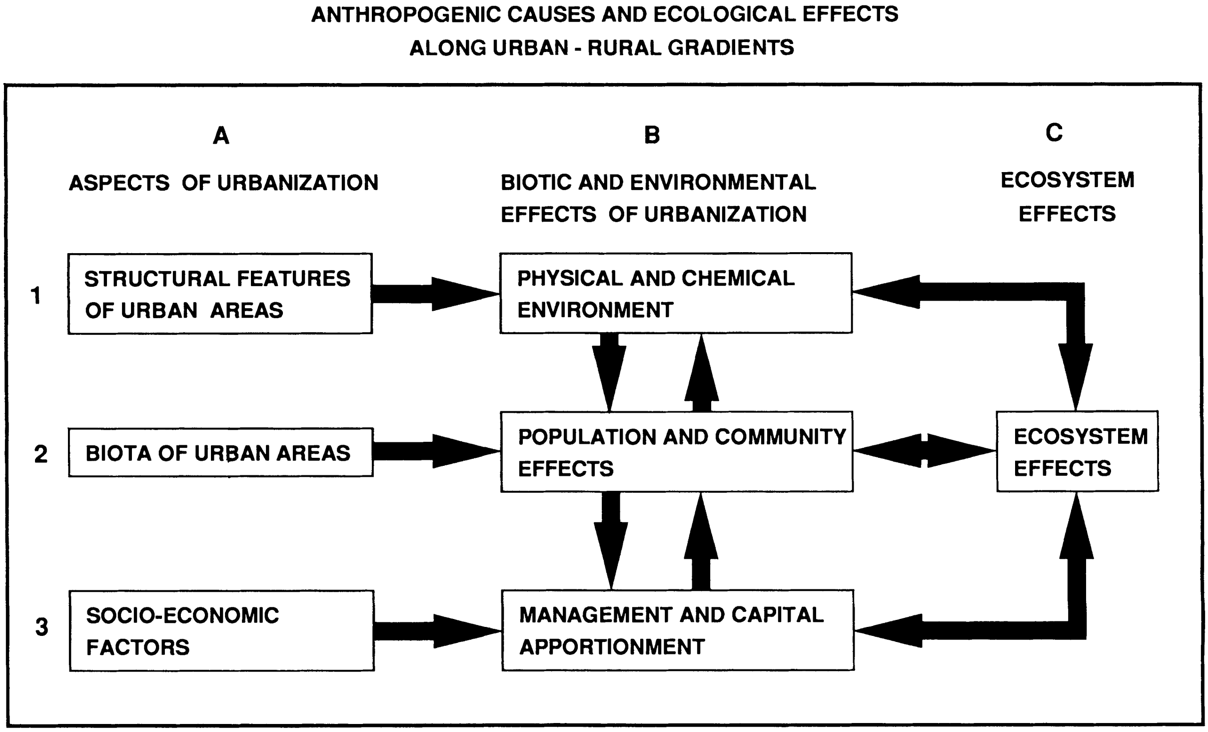

FIG. 2. A composite model of the effects of urbanization on ecological phenomena. The three columns are abstracted from the details of Tables 1 and 2, and the arrows indicate causal linkages between the features of urban areas (column A), as inputs, and the ecological phenomena (columns B, C) as results. The focus of the research program would be on the phenomena represented by rows 1 and 2, although the results would be helpful in decisions concerning societal phenomena represented by row 3. Feedbacks from columns B and C to A would receive attention in research building on that under the scope of this program.

is more uneven and the number and connectedness of treefall gaps differs from rural forests in the region. Furthermore, the fauna and its interactions (e.g., predation, Churcher and Lawton 1987) differ in urbanized areas. These conditions indicate that organization and dynamics of the forests should differ along the gradient.

Once the composition, size structure, and stand architecture are adequately documented, attention can turn to questions such as these: Is the regeneration of current or prior dominants limited in forests at the urban end of the gradient? What are the compositional or architectural correlates of regeneration success or failure? What are the abiotic, biotic, and anthropogenic causes of regeneration patterns? Do changes in the animal community have direct or indirect effects on the plant community dynamics by changing herbivory, predation, or dispersal relations of the plants? How do human perceptions, values, and behaviors affect the dynamics and persistence of forest communities along the gradient?

Landscape ecology

Landscape ecology is empirically a young discipline. Therefore, the questions that may be asked of it in the context of urban–rural gradients are quite exploratory. Indeed, such questions may have a stimulatory effect on landscape ecology as a whole. In the spirit of an exploratory analysis, assume that the elements of a landscape are more distinct toward the urban end of the gradient (Godron and Forman 1983). Note, however, that the pattern of distinctness can be determined by direct measurement of aerial photographs and maps, so that whether distinctness of patches increases or decreases monotonically, or is humped in some middle distance on the gradient, is a simple empirical matter. Illustrative questions that may follow upon the pattern analysis include the following: Is dispersal of plants, over equivalent distances, more limited in urban than rural ranges of the gradient? Is any such change a direct result of the activities of people (including vehicles, pets, and pests) or some indirect effect of the size, shape, and arrangement of landscape elements? How does size, shape, distance, and arrangement of patches relate to their species composition and to ecosystem processes within them?

A Conceptual Model for the Ecology of Urban–Rural Gradients

Because the study of ecology along urban–rural gradients is new, a framework to help guide the design

TABLE 2. An elaboration of the environmentally and biotically relevant effects of the features of urbanization (Table 1).

Physical and chemical environment
Local climate
Air pollution
Hydrologic changes
Water pollution
Soil changes and earth movement
Population and community characteristics
Altered disturbance regimes
Introduced species
Increase in morbidity
Altered assimilation
Altered reproductive status
Changes in growth rates
Phenological changes
Reduced longevity
Social and behavioral changes
Genetic drift and selection
Population size and structure
Altered successions
Reduced richness
Landscape fragmentation
Ecosystem structure and function
Debris dams
Forest floor
Sediment loading
Patchiness
Layering of vegetation
Productivity
Nutrient flux
Decomposition
Nutrient retention
Loss of redundant pathways
Loss of compartments
Alteration of equilibria
Management and capital apportionment

and integration of studies is required. The framework must account for: (A) the factors that constitute urbanization, (B) the effects of urbanization on the biota and physical environment, and (C) the resultant effects on ecosystems (Fig. 2). The constituent factors of urbanization and their biotic and environmental effects are each divisible into three realms. In order of increasing complexity, these realms are (1) physical structure, (2) biotic components, and (3) human culture and institutions (Fig. 2). The physical and chemical environment and the dynamics of natural and seminatural populations and communities can be affected by urbanization in many ways (Table 2). The conceptual model serves as a framework that will be filled in as the study of ecology in this new context matures. Ultimately, specific mechanistic, predictive, or explanatory models will be constructed to quantitatively describe the interactions and components of the conceptual framework (Fig. 2).

Ecologists usually only study two parts of the three-part model (Fig. 2b, c) and do so most often in non-urban systems. Explicit study of the aspects and features of urbanization (Fig. 2a) as well as their effects (Fig. 2b, c) is an underutilized area for ecological research, but one of increasing importance given the extension and magnitude of anthropogenic effects today.

CONCLUSION

The growth of metropolitan areas in North America and indeed worldwide indicates that knowledge of ecosystems under the influence of urbanization can only become increasingly important. The magnitude and nature of the change in the physical, chemical, and biotic environments that are associated with urbanization provide an unprecedented suite of "experimental manipulations" that ecologists can utilize. We propose a framework to guide the design and integration of ecological studies along urban–rural gradients and indicate its utility for addressing basic ecological questions. Finally, we suggest that the study of urban–rural gradients provides a new context in which to integrate humans as critical components of ecological systems. The results of these studies will not only contribute to our understanding of basic ecological principles, but are critical to the ecologically sound management of human-dominated ecosystems.

ACKNOWLEDGMENTS

We would like to thank J. Brown, G. Guntenspergen, J. Koch, P. Matson, P. Vitousek, and W. Zipperer for their comments and suggestions on the manuscript. G. Likens, G. Lovett, and R. Pouyat made helpful suggestions on earlier versions of the manuscript. Contribution to the program of the Institute of Ecosystem Studies, The New York Botanical Garden.

LITERATURE CITED

Adams, S., B. R. Strain, and M. S. Adams. 1970. Water-repellent soils, fire and annual plant cover in a desert shrub community in southeastern California. Ecology **51**:696–700.

Airola, T. M., and K. Buchholz. 1984. Species structure and soil characteristics of five urban sites along the New Jersey Palisades. Urban Ecology **8**:149–164.

Alig, R. J., and R. G. Healy. 1987. Urban and built-up land area changes in the United States: an empirical investigation of determinants. Land Economics **63**:215–226.

Andrews, W. A., and J. L. Cranmer-Byng. 1981. Urban natural areas: ecology and preservation. Environmental Monograph Number 2. Institute for Environmental Studies, University of Toronto, Toronto, Canada.

Austin, M. P. 1987. Models for the analysis of species' response to environmental gradients. Vegetatio **69**:35–45.

Bagnell, R. G. 1979. A study of human impact on an urban forest remnant: Redwood Bush, Tawa, near Wellington, New Zealand. New Zealand Journal of Botany **17**:117–126.

Bornkamm, R., J. A. Lee, and M. R. D. Seaward. 1982. Urban ecology. Blackwell Scientific, Oxford, England.

Bourne, L. S., and J. W. Simmons. 1982. Defining the area of interest: definition of the city, metropolitan areas and extended urban regions. Pages 57–72 *in* L. S. Bourne, editor. Internal structure of the city. Oxford University Press, New York, New York, USA.

Boyden, S. V. 1977. Integrated ecological studies of human settlements. Impact of Science on Society **27**:159–169.

Boyden, S. V., and S. Millar. 1978. Human ecology and the quality of life. Urban Ecology **3**:263–287.
Churcher, P. B., and J. H. Lawton. 1987. Predation by domestic cats in an English village. Journal of Zoology **212**: 439–455.
Debano, L. F. 1971. The effects of hydrophobic substances on water movement in soil during infiltration. Soil Science Society of America Proceedings **35**:340–343.
Dickinson, R. E. 1966. The process of urbanization. Pages 463–478 *in* F. F. Darling and J. P. Milton, editors. Future environments of North America. Natural History Press, Garden City, New York, USA.
Dorney, J. R., G. R. Guntenspergen, J. R. Keough, and F. Stearns. 1984. Composition and structure of an urban woody plant community. Urban Ecology **8**:69–90.
Ehrenfeld, D. W. 1970. Biological conservation. Holt, Rinehart, & Winston, New York, New York, USA.
Fox, R. 1987. Population images. United Nations Fund for Population Activities.
Frey, H. T. 1984. Expansion of urban area in the United States: 1960–1980. United States Department of Agriculture Economic Research Service Staff Report Number **AGES830615**.
Gill, D., and P. Bonnett. 1973. Nature in the urban landscape: a study of city ecosystems. York, Baltimore, Maryland, USA.
Godron, M., and R. T. T. Forman. 1983. Landscape modification and changing ecological characteristics. Pages 12–28 *in* H. A. Mooney and M. Godron, editors. Disturbance and ecosystems. Springer-Verlag, New York, New York, USA.
Haub, C., and M. M. Kent. 1989. 1989 world population data sheet. Population Reference Bureau, Washington, D.C., USA.
Hobbs, E. 1988. Using ordination to analyze the composition and structure of urban forest islands. Forest Ecology and Management **23**:139–158.
Kolasa, J., and S. T. A. Pickett. 1990. Ecological systems and the concept of biological organization. Proceedings of the National Academy of Sciences (USA) **86**:8837–8841.
Kunick, W. 1982. Comparison of the flora of some cities of the central European lowlands. Pages 13–22 *in* R. Bornkamm, J. A. Lee, and M. R. D. Seaward, editors. Urban ecology. Blackwell Scientific, Oxford, England.
McDonnell, M. J. 1988. A forest for New York. Public Garden **3**:28–31.
McGhie, D. A., and A. M. Posner. 1981. The effect of plant top material on the water repellence of fired sands and water repellent soils. Australian Journal of Agricultural Research **32**:609–520.
Mumford, L. 1956. The history of urbanization. Pages 382–400 *in* W. Thomas, editor. Man's role in changing the face of the earth. University of Chicago Press, Chicago, Illinois, USA.
Noyes, J., and D. Proqulske. 1974. Wildlife in an urbanizing environment. Cooperative Extension Service, University of Massachusetts, Amherst, Massachusetts, USA.
Numata, M. 1977. The impact of urbanization on vegetation in Japan. Pages 161–171 *in* A. Miyawaki and R. Tuxen, editors. Vegetation science and environmental protection. Proceedings of the International Symposium in Tokyo on Protection of the Environment and Excursion on Vegetation Science through Japan. 5–7 June. Maruzen, Tokyo, Japan. Chiba University, Chiba, Japan.
O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. A. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.
Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
Reeder, C. J., and M. F. Jurgensen. 1979. Fire induced water repellency in forest soils of upper Michigan. Canadian Journal of Forest Research **9**:369–373.
Roberts, D. W. 1987. A dynamical systems perspective on vegetation theory. Vegetatio **69**:27–33.
Rudnicky, J. L., and M. J. McDonnell. 1989. Forty-eight years of canopy change in a hardwood-hemlock forest in New York City. Bulletin of the Torrey Botanical Club **116**: 52–64.
Stearns, F., and T. Montag. 1974. The urban ecosystem: a holistic approach. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, USA.
Stevens, G. C. 1989. The latitudinal gradient in species range: How so many species coexist in the tropics? American Naturalist **133**:240–256.
Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillero Vilcabamba, Peru. Ecology **52**:23–40.
Ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18**:272–327.
United States Bureau of Census. 1980. Census user's guide. United States Department of Commerce, United States Government Printing Office, Washington, D.C., USA.
Vayda, A. P. 1983. Progressive contextualization methods for research in human ecology. Human Ecology **11**:265–282.
White, C. S., and M. J. McDonnell. 1988. Nitrogen cycling processes and soil characteristics in an urban versus rural forest. Biogeochemistry **5**:243–262.
Whitney, G. G., and S. D. Adams. 1980. Man as a maker of new plant communities. Journal of Applied Ecology **17**: 341–448.
Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Reviews **49**:207–264.