Ecosystem Processes Along an Urban-to-Rural Gradient

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Abstract In order to understand the effect of urban development on the functioning of forest ecosystems, during the past decade we have been studying red oak stands located on similar soil along an urban-rural gradient running from New York City ro rural Litchfield County, Connecticut. This paper summarizes the results of this work. Field measurements, controlled laboratory experiments, and reciprocal transplants documented soil pollution, soil hydrophobicity, litter decomposition rates, total soil carbon, potential nitrogen mineralization, nitrification, fungal biomass, and earthworm populations in forests along the 140 × 20 km study transect. The results revealed a complex urban-rural environmental gradient. The urban forests exhibit unique ecosystem structure and function in relation to the suburban and rural forest stands; these are likely linked to stresses of the urban environment such as air pollution, which has also resulted in elevated levels of heavy metals in the soil, the positive effects of the heat island phenomenon, and the presence of earthworms. The data suggest a working model to guide mechanistic work on the ecology of forests along urban-to-rural gradients, and for comparison of different metropolitan areas.

Keywords: urban · rural · forests · gradients · ecosystems

Introduction

The conversion of natural or agricultural landscapes throughout the world to highly modified urban landscapes is expected to continue and many urbanized areas are expected to become even more highly modified (Alig and Healy, 1987; Richards, 1990; Douglas, 1994). The need for comprehensive studies of the ecological impacts of urbanization is great (Brown and Roughgarden, 1989; Rogers, 1994; Penner, 1994). In 1989, 74% of the U.S. population (203 million people) resided in urban areas and that number is expected to increase to more than 80% by the year 2025 (Fox, 1987; Alig and Healy, 1987; Haub and Kent, 1989). Between 1960 and 1980, urban land in the United States increased by 22 million acres (Frey, 1984) resulting in the conversion of cropland, pastures, and forests into urban and suburban environments.

Ecologists in North America, however, have historically been reluctant to study ecological systems in urban environments because they are perceived as ‘unnatural’ and contain such problems unknown disturbance histories, multiple stresses, and lack of dedicated research sites (Cairns, 1987, 1988; Ludwig, 1989; McDonnell and Pickett, 1990; Botkin, 1990). Thus, at a time

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when legislators, managers, scientists modeling global change, and the general public critically need ecological information from urban areas there is relatively little available.

Because ecologists have not historically worked in areas populated by humans, important terminology and concepts related to urban environments have been developed by geographers, social scientists, anthropologists, and economists and may not always be ecologically operative. Therefore, commonly used terms as ‘urban’ and ‘rural’ have multiple meanings and relate to a variety of conditions such as land cover, population density, the amount of impermeable surfaces, and cultural practices. For the purpose of this paper, we use the geographer’s definition of urban based on the number of humans per hectare (ha). urban areas are defined as having more than 6.2 people per ha whereas rural areas have 1 to <1 person per ha (U.S. Bureau of Census, 1980; Bourne and Simmons, 1982). Areas described as suburban typically have human population densities between the urban and rural levels. The high density of humans in urban areas typically results in large-scale modification of the environment and a tremendous concentration of food, water, energy, materials, sewage, pollution, and garbage which we collectively categorize as urban land use (Godron and Forman, 1983; Roodman, 1996). At the other end of the land-use spectrum are rural environments that are sparsely populated with humans and consequently exhibit less built-on land and lower concentrations of energy, materials, water, and waste products (Godron and Forman, 1983).

The conversion of rural land use to urban land use is referred to as urbanization and occurs over time. This paper does not address the ecological consequences of urbanization over time, but instead focuses on the effects of urbanization in a spatial context. We are specifically interested in quantifying changes in the structure and function of forests embedded in a range of land-use types from existing urban to rural landscapes. Our measure of urbanization in space is the distance from the urban core which is supported by our land use analysis of the study area. The forests closest to the New York City end of the transect are considered to be more urbanized than those at the rural end.

This paper is a synthesis of more than a decade of research on forest ecosystems along an urban-rural land use gradient running from densely populated New York City north to rural Litchfield County, Connecticut. We feel that the use of standard gradient analysis techniques provides a new approach for addressing both basic ecological questions and practical environmental problems facing urban areas (McDonnell *et al.*, 1993). By quantifying changes in ecosystem structure and function in relationship to varying levels of urbanization, we can obtain a greater understanding of the nature of urban impacts on natural ecosystems which will assist us in developing important new research questions and management strategies.

Ecologists have effectively studied natural gradients of soil moisture, elevation, and salinity to understand the relationship between environmental variation and the structure and function of ecological systems, including populations, communities, and ecosystems (Whittaker, 1967; Siccama, 1974; Pickett and Bazzaz, 1976; Peet and Loucks, 1977; Austin, 1987; Keddy, 1989; Vitousek and Matson, 1990). The gradient paradigm also applies to urban environments (McDonnell and Pickett, 1990; McDonnell *et al.*, *1993*). Urban areas in the United States typically have a highly modified and densely populated urban core surrounded by asymmetric rings of diminishing landscape modification (Dickinson, 1966; Forman and Godron, 1986; Berry, 1990). The resulting array of natural and human-modified ecosystems within a metropolitan area can be conceived of as a readily measurable gradient of land use and a more complex gradient of urban effects (McDonnell and Pickett, 1990; McDonnell *et al.*, 1993; Medley *et al.*, 1995). Thus, the gradient paradigm is a useful organizing tool for research on the ecological consequences of urbanization. Since the concept of urban-rural gradients was introduced (McDonnell and Pickett, 1990) it has been effectively used to study a variety of ecological issues in urbanized areas throughout the world, including avian diversity (Blair, 1996) and richness (Jokimaki and Suhonen, 1993), air pollution effects on moss-dwelling animals (Steiner, 1994), heavy metal accumulation by mosses (Gupta, 1995), and lepidoptera population diversity and variability (Wolda *et al.*, 1994).

A Model for Assessing Anthropogenic Causes and Ecological Effects

The structure of metropolitan areas and their fringes consists of a variety of components, ranging from totally built environments to 'natural' or seminatural areas (Stearns and Montag, 1974). Ecological studies of urban areas can focus on several scales including the metropolitan area as a whole, the city core, or a natural area within a city. Natural areas are defined as ecosystems which persist primarily because of natural processes of plant establishment, water availability, nutrient cycling, and plant-animal interactions with minimal human manipulation (e.g., wooded natural areas in New York City parks, lakes, ponds, streams, etc.) (McDonnell, 1988). To facilitate the study of the ecology of urbanization, the individual components (e.g., structures, physical and chemical environments, populations, communities, and ecosystems) must be quantified, and correlations among them assessed. By doing so, the ecologically important impacts of urban development and change on natural areas can be determined. McDonnell and Pickett (1990) proposed a model of the effects of urbanization on ecological phenomena that includes: a) aspects of urbanization, b) biotic and environmental effects of urbanization, and c) ecosystem effects (Fig. 1). We will use this model to illustrate the utility of the gradient paradigm in studying the structure and function of forests (i.e., natural areas) along urban-rural gradients.

The Study Site

As previously stated, we have focused our research on urban-to-rural gradients on a 140-km transect running from highly urbanized Bronx County, New York, to rural Litchfield County, Connecticut. (McDonnell *et al.*, 1993) (Fig. 2). Manhattan and the study area to the north constitute

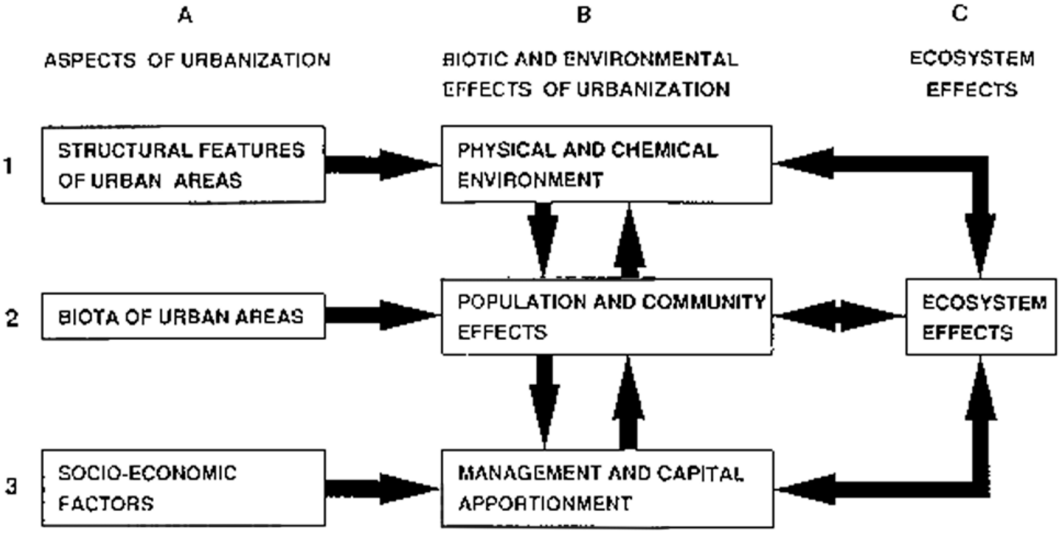

Fig. 1 A composite model of the effects of urbanization on ecological phenomena. The three columns represent relevant components of urban-rural gradients. The arrows indicate causal linkages between the features of urban areas (column A) as inputs, and the ecological phenomena (columns B, C) as results. Ecological research is focused primarily on the phenomena represented by rows 1 and 2, whereas the results would be helpful in decisions concerning societal phenomena represented by row 3. Feedbacks from columns B and C to A would be useful in developing strategies to reduce the environmental impact of urbanization. (Modified from McDonnell and Pickett, 1990)

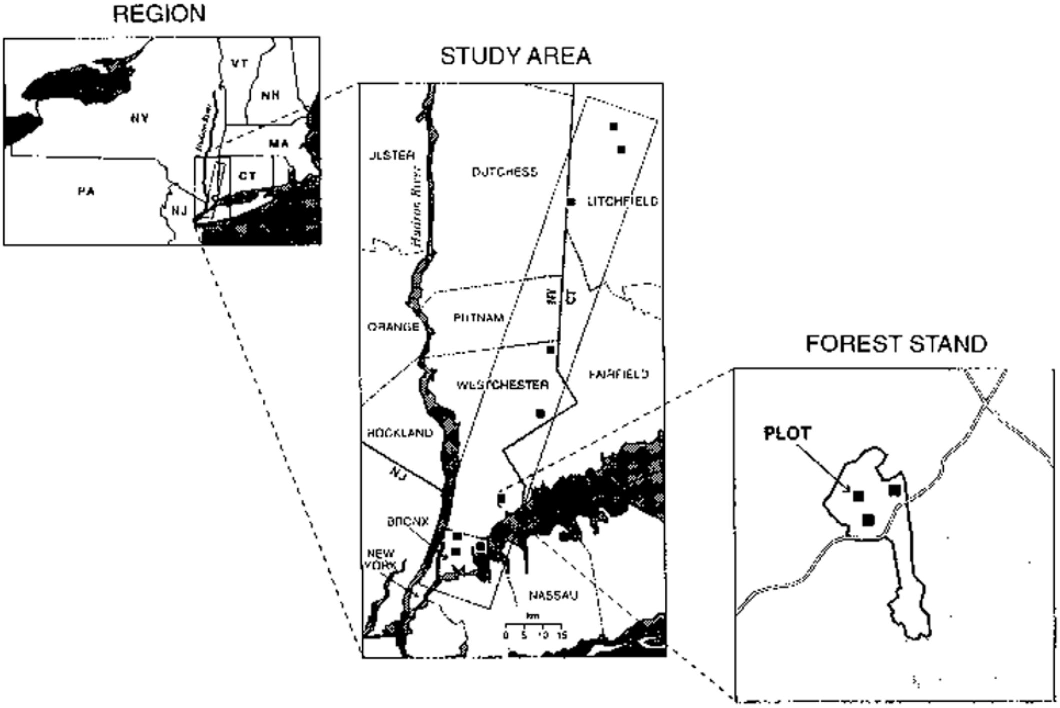

Fig. 2 A map of the New York City Metropolitan Area showing the location of the 20 km wide by 140 km long transect used to study the structure and function of forests along the urban-rural gradient. Ecological studies can focus on a variety of scales ranging from the metropolitan region, landscape unit to forest site. (Modified from McDonnell and Pickett, 1990)

the southern portion of the Northeastern Upland Province (Broughton *et al.*, 1966). The study transect was centered on that part of the landscape with bedrock consisting of metamorphosed and dissected crystalline rocks which were separated into various formations classified by their composition of schist, granite, and gneiss (Schuberth, 1968). Upland soils in the study area are classified as Typic or Lithic Dystrochrepts, loamy, mixed, mesic subgroups (Gonick *et al.*, 1970; Hill *et al.*, 1980).

To control for potentially confounding factors, such as differences in parent material, soil moisture regimes, stand age, species composition, and soil texture, only forests exhibiting the following conditions were considered for study: 1) similar topography and soil type to at least the U.S. Department of Agriculture (USDA) subgroup classification category (Soil Survey Staff, 1975); 2) oak dominated community (including at least one of the following species *Quercus rubra, Quercus veluiina, Quercus alba*, and *Quercus coccinea*) with similar species composition across sites; 3) minimum stand age of 60 years; 4) a closed canopy; and 5) no evidence of recent severe anthropogenic disturbances such as soil excavation or tree cutting.

Nine forest study sites were established along the transect (Fig. 2). They were stratified to have three forests representing each of the urban, suburban, and rural regions of the gradient. Within each forest study site three 20 m × 20 m plots were randomly established at least 50 m from the edge of the forest patch giving a total of 27 plots along the transect (Fig. 2).

Aspects of Urbanization

Landscape structure and human population densities

We have coarse-resolution data to characterize the overall patterns of change along the $20 \times 140\,\mathrm{km}$ transect. Population characteristics, summarized by county subdivisions, have been plotted along a line positioned in the middle of the urban-rural belt transect. State and interstate highways, with traffic counts averaged for major road sections, were mapped at 1:250,000. From this map we computed a mean of annual daily traffic averages and a measure of connectivity (β = no. road segments/no intersections; see Haggett *et al.*, 1977) for the highways within $20 \times 5\,\mathrm{km}$ sections along the transect. The U.S. Geological Survey (USGS) land use-land cover digital data were imported into IDRISI (a grid-based geographic analysis system produced by the Clark University Graduate School of Geography) and rasterized into a grid-cell map. The area of the grid cells, 17.6 ha, closely approximates the original scale of generalization used in the original classification of rural localities ($\sim 16\,\mathrm{ha}$; see U.S. Geological Survey, 1986). Land use and landscape fragmentation were compiled for ten $\sim 77\,\mathrm{km}^2$ land units randomly selected from the rasterized map. We used multiple sampling techniques to determine a most effective approach, considering the variety of spatial data applicable to the project (Medley *et al.*, 1995).

Preliminary analyses document a complex urban-to-rural gradient. Human population density, traffic volume, and the percentage of built-up land (i.e., urban and residential) decline, whereas the percentage of forest land and the mean size of forest patches increase, in a linear or logarithmic trend away from the urban New York City core (Medley *et al.*, 1995). A sharp transition from an urban matrix to a forest matrix occurs along the urban-rural transect in this agriculturally unproductive region. Conversely, 1960–1990 population growth, highway connectivity, and the structural heterogeneity of the landscape, show quadratic relationships to urban-rural distance (Medley *et al.*, (1995). These findings suggest that urban exposure parallels the transect, but the changes or disturbances associated with urbanization show a complex spatial pattern not clearly related to urban-rural distance alone (Medley *et al.*, 1995).

Biotic and Environmental Effects of Urbanization

Physical and chemical environment

The climate of the region is characterized by warm, humid summers and cold winters with average annual air temperatures ranging from 12.5°C in New York City to 8.5°C in northwestern Connecticut (National Oceanic and Atmospheric Administration [NOAA], 1985). A close examination of the temperatures recorded from 1985 to 1991 at NOAA/National Weather Service sites located at 0, 25, 57, 112, and 140 km along the transect revealed that the mean monthly temperatures at the 0-km site, which is the urban core, are typically 2–3°C warmer than any of the other locations (McDonnell *et al.*, 1993). This reflects, in part, the well documented heat island phenomenon occurring in urban areas throughout the world (Bornstein, 1968; Berry, 1990).

Precipitation ranges from an average annual total of 108 cm in New York City to 103 cm in north-western Connecticut (NOAA, 1985). Precipitation is evenly distributed throughout the year (McDonnell *et al.*, 1993). Air quality is poor at the urban end of the gradient and improves in rural areas as illustrated by the decline in particulate sulfate and total particulate levels with increasing distance from the urban core (New York State Department of Environmental Conservation, 1989; Gradedel and Crutzen 1989).

Although many features of the forest soils along this urban-rural gradient are similar, we discovered elevated levels of lead, copper, and nickel in forests at the urban end of the gradient, declining to background levels in rural sites (Pouyat and McDonnell, 1991; Pouyat *et al.*, 1995). We also found soil hydrophobicity (i.e., water repellency) as measured by contact angle of a water droplet to be highest in forests at the urban end of the gradient (White and McDonnell, unpubl. data). Finally, analysis of the forest floor leaf litter along the transect indicated that mean depth, mass, and density of the leaf litter layer increased with increasing distance from the urban core (Kostel-Hughes, 1995; Kostel-Hughes *et al.*, 1996).

Population and Community Attributes

Forests in the urban end of the transect have lower stem densities, depauperate understories, and contain an increasing proportion of non-native species in the sapling and seedling size classes than similar forests in rural areas (Rudnicky and McDonnell, 1989; McDonnell *et al.*, 1990; McDonnell and Roy, 1996; McDonnell, unpubl. data). Studies of the soil seed bank in urban forests also reveal the presence of non-native woody plant species, but at relatively low densities (Kostel-Hughes, 1995).

Pouyat *et al.* (1994a) found that soil microinvertebrates, of which they included the taxonomic groups Mesostigmata, Orbatida, Collembola, and other microinsects, abundances were higher in the rural forests than in either the urban or suburban sites during the fall season, but exhibited no significant differences during the spring. Red oak litter placed on the forest floor of the study sites along the transect by Pouyat *et al.* (1994a) also exhibited a measurable difference in fungal activity. Rural forests had the highest total fungal hyphal length (i.e., abundance) after 36 weeks of exposure as compared with the suburban and urban sites. Between leaf drop and mid-winter, fungi appeared to have grown more rapidly on litter in the rural sites than either the suburban or urban forests. Both fungivous microinvertebrates and litter fungi were inversely correlated with soil heavy metal concentrations (Pouyat *et al.*, 1994a).

An assessment of earthworm populations in forests along the transects by Steinberg *et al.* (1996, in press) revealed high numbers and biomass of earthworms in the urban forests with relatively few in forests at the rural end of the transect. Steinberg *et al.* (in press) report that urban forests had 25.1 worms m^{-2} and 2.16 g of worms m^{-2} whereas the rural forests had only 2.1 worms m^{-2} and 0.05 g of worms m^{-2}. The reduced leaf litter depth, mass and density of the forest floor (O_2 horizon) (Kostel-Hughes, 1995), and increased organic matter levels at depth (Pouyat *et al.*, 1995) provide further support for increased earthworm activity in the urban forests along the study transect.

These studies are not suggesting that rural forests with earthworms do not exist along the transect or that every urban forest has abundant earthworm populations. However, the forests on our study transect are in previously glaciated areas. No native earthworm species occur in these areas, and the prevalence of non-native species may depend largely on the degree of human activity (Sam James, Maharishi International University, pers. comm.; Steinberg *et al.*, 1996, in press). Therefore, our observations of low earthworm densities in the rural sites are not unreasonable, and for our gradient it appears that the absence of earthworms in the rural sites and high densities in the urban sites is a real dichotomy that can explain, in part, some of the differences in nutrient cycling parameters described below.

Ecosystem Effects

We chose to focus this area of research on two key components of forest ecosystems that are likely to vary in response to the complex gradients that extend from a dense urban core to the surrounding countryside: plant litter dynamics and nitrogen cycling. Foliar litter decomposition is an ideal feature of ecosystems to examine because it integrates many features of the abiotic and biotic environments. Litter decomposition affects plant community regeneration (Facelli and Pickett, 1990), is a critical bottleneck in determining ecosystem nutrient flow and therefore availability of resources for higher plants in a community (Coleman, 1986; Monk and Day, 1988), is an important site of heavy metals incorporation into ecosystems (Van Hook and Shults, 1977; Tyler, 1978), and provides both a habitat and resource for fungi, bacteria, and invertebrates (Choudhury, 1988; Seastedt and Crossley, 1983). Litter decomposition, consequently integrates the effects of resource quality, environmental factors and activities of decomposer organisms on nutrient cycling, thereby serving as an easily measured indicator of the impact of urbanization on an important ecosystem function.

Forest nitrogen dynamics have been studied extensively in the Northeastern United States and there is a large body of literature that suggests that increased anthropogenic inputs of nitrogen in urban environments should have complex non-linear effects on plants, microbes, and soil chemistry (Friedland *et al.*, 1984; Nihlgard, 1985; Agren and Bosatta, 1988; Aber *et al.*, 1989). Aber *et al.* (1989) made a number of specific predictions of ecosystem-level responses to constant, elevated nitrogen inputs continued over many years. They emphasized the pivotal nature of the onset of significant nitrification, when more nitrogen is mineralized than can be taken up by plants and microbes. Nitrification could precipitate decreases in fine root biomass and increases in NO_3 leaching below the rooting zone (Aber *et al.*, 1989). McNulty *et al.* (1990) documented a pattern of increased nitrification (when expressed as a fraction of nitrogen mineralization) across a transect from southern Maine to northern New York, a gradient characterized by an almost twofold increase in nitrogen wet deposition. McColl and Bush (1978) have shown increased nitrification and NO_3 leaching in forests attributable to nitrogen deposition from the urban area downwind of San Francisco and Johnson *et al.* (1991) have reported the same phenomena in high-elevation spruce forests of North Carolina, which receive elevated levels of nitrogen deposition from rain, dry deposition, and cloud water.

Our initial hypothesis concerning decomposition and nitrogen-mineralization rates along the transect was based primarily on the soil characteristics showing high levels of heavy metals in urban forest soils and the biotic measurements which indicated reduced soil fungi and microinvertebrates in the forests at the urban end of the transect. This would be consistent with the widely held view that forests in urban environments are under stress and should exhibit reduced ecosystem function (Goudie, 1990). Thus, our initial hypothesis of ecosystem processes along our transect predicted that decomposition rates, nitrogen-mineralization rates, and nitrification rates would be lower in forests in the urban environment.

Litter decomposition and carbon dynamics

Litter decomposition rates in forests along the transect were determined using standard litter bag techniques (Bocock, 1964; Freedman and Hutchinson, 1979). The initial experiment used a reference litter of sugar maple (*Acer saccharum*) collected from a rural site and, contrary to expectations, revealed that decomposition rates were higher in forests at the urban end of the transect (Pouyat, 1992; McDonnell *et al.*, 1993). To test whether decomposition rates were controlled by site environment or litter quality, reciprocal red oak (*Q. rubra*) litter transplants were performed between urban and rural sites on the transect. The results of this study indicated that both urban and rural litter decomposed faster in urban vs. rural sites (Pouyat *et al.*, 1996, in press). The rural litter, however, consistently decomposed faster than the urban litter in all sites. This suggests that the rural litter is of higher quality than the urban litter.

The differences in decomposition rates and litter quality between the urban and rural forest stands just described, coupled with the variations in the physical, chemical, and biotic environments along the study transect presented in previous sections, suggested that the flow of carbon between plants and microbial communities may be quite different in urban vs. rural forests. Groffman *et al.* (1995) examined the carbon dynamics of forests along the study transect in detail, separating the soil carbon into four pools: 1) readily mineralizable carbon with a turnover time of days to weeks; 2) labile carbon with a turnover time of weeks to months; 3) potentially mineralizable carbon with a turnover time of months to years; and 4) passive carbon which is very recalcitrant with a turnover time of years to decades to centuries. They discovered that the urban forests had lower labile carbon and higher total passive carbon than the rural forests (Groffman *et al.*, 1995). Rural forests also had higher pools of both readily mineralizable and potentially mineralizable carbon (Groffman *et al.*, 1995). Groffman *et al.* proposed that high total passive carbon in the urban forest soils are most likely due to three factors: 1) high decomposition rates in urban forest which would deplete the labile carbon pool; 2) air pollution, especially ozone damage, which may lead to the creation of more passive carbon; and 3) the presence of earthworms, which would expedite the retention of organic matter in soil aggregates. They concluded from this study that, over a long period of time, urban forests along the transect have a potential for sequestering and storing more carbon than the rural forests, but the lower levels of labile carbon in the urban stands could result in lower rates of microbial activity in the urban forest soils.

Nitrogen dynamics

Several studies have been conducted to determine the nature of the nitrogen dynamics of forests along the transect (White and McDonnell, 1988; Pouyat, 1992; Pouyat *et al.*, 1994b; Pouyat *et al.*, 1996, in press; Goldman *et al.*, 1995; Steinberg *et al.*, 1996, in press). Measurements of nitrogen-mineralization and nitrification rates were made both in the laboratory and *in situ* in buried bags during the growing season (April–November). The laboratory incubations allowed us to control moisture and temperature which we knew varied along the transect. During the past 5 years nitrogen-mineralization and nitrification rates have been obtained for the A horizon, and for the forest floor and mineral soil combined in forests along the transect (O plus A Horizons).

Net nitrogen-mineralization and nitrification rates of the A horizon, as measured in the laboratory incubations (i.e., net potential nitrogen mineralization) and *in situ* in buried bags, were highest in the urban forests in comparison to the rural forests (Pouyat, 1992; Pouyat *et al.*, 1994b; Pouyat *et al.*, 1996, in press). In addition, nitrification accounted for close to 50% of the total nitrogen-mineralization measured in urban forest soils as compared to only 20% for the rural soils (Pouyat, 1992).

In subsequent studies of mineralization and nitrification rates of forest soils along the transect the humus layer was included in the soil samples (O plus A Horizon). These studies revealed results contradictory from those mentioned above. Net potential mineralization rates were higher in the rural forest stands as opposed to the urban stands (Goldman *et al.*, 1995; Pouyat *et al.*, unpubl. data; Groffman *et al.*, unpubl. data). Nitrification rates in urban forest soils, on the other hand, were still higher than in the rural forest soils (Goldman *et al.*, 1995, Pouyat *et al.*, unpubl. data, Groffman *et al.*, unpubl. data). These high nitrification rates that occur in urban soils even when nitrogen-mineralization rates are low, appear to be the result of a history of earthworm activity (Bohlen *et al.*, 1996; Pouyat *et al.*, 1996). The discrepancies between nitrogen-mineralization and nitrification rates from A horizon samples vs. O plus A horizon samples in urban and rural forest soil samples can be explained simply by the amount of organic matter available for microbial degradation. Urban forest A horizon samples have higher organic matter mixed throughout the sample due to the presence of large numbers of earthworms in comparison to the rural forest soils (Steinberg *et al.*, 1996, in press). Those soil samples with higher organic matter (i.e., urban forest soils) would exhibit higher nitrogen-mineralization and nitrification rates due to the increased availability of nitrogen and carbon. Following this reasoning, soil samples that contain both the O and A horizons would have higher nitrogen-mineralization and nitrification rates than samples that contain only the A horizon. Because the rural forests have a more developed humus layer as compared to the urban forests, we would expect that nitrogen-mineralization and nitrification rates would be higher in the rural forest stands (Pouyat *et al.*, 1995).

The low available nitrogen, low labile carbon pools, and high passive carbon pools in the urban forest soils (O plus A horizon) in relation to the rural forest appear to also have an effect on trace gas fluxes. Laboratory and field measurements of methane (CH_4) consumption rates in urban, suburban and rural forest soils along the study transect indicated that urban forest soils consumed 30% less CH_4 than either the suburban or rural stands (Goldman *et al.*, 1995). The authors suggest that the low amount of labile carbon in the urban forest soils adversely influences the soil microbial community that is the primary cause of CH_4 consumption in forest soils.

The Structure and Function of Oak Forest Ecosystems Along an Urban-rural Gradient

The application of the urban-rural gradient concept to determine the influence of urbanization on the structure and function of oak forest ecosystems has been successful in obtaining a new understanding of the effects of urbanization on ecological phenomena. Using our initial model of anthropogenic causes and ecological effects along urban-rural gradients (Fig. 1), especially levels 1 and 2, we obtained somewhat unexpected results that revealed unique interactions between the three major components of the model: ‘aspects of urbanization,’ ‘biotic and environmental effects of urbanization,’ and ‘ecosystem effects’ (Fig. 3). The structural features of the landscape (e.g., land-use patterns, roads, etc.), varied significantly along the study transect with the urban end having more built structures and surfaces such as roads in comparison to rural Litchfield County. There were also measurable differences in the physical and chemical environment along the study transect with the urban end exhibiting high levels of air pollution and soil heavy metals as well as increased temperatures in comparison with the rural end of the transect. These results confirm that there is an underlying complex environmental gradient that runs from the New York City urban core to rural Litchfield County, Connecticut (McDonnell *et al.*, 1993).

The literature on the detrimental effects of poor air quality (e.g., high levels of SO_2, sulfate, ozone, etc.), elevated levels of soil and forest floor heavy metals, and low water availability such as those caused by hydrophobic soils, support the commonly held ecological belief that forest ecosystems in urban environments would have low species diversity, low productivity, slow decomposition rates and low nitrogen-mineralization rates (Tyler, 1975; Lepp, 1981; Smith, 1990; Treshow, 1984; Hutton, 1984; Goudie, 1990; Findlay and Jones, 1990).

In our study area, the heavy metal levels in urban forest stands approach or exceed those levels found to affect soil invertebrates (Bengtsson and Tranvik, 1989), macrofungi (Freedman, 1989), and soil microbial processes (Baath, 1989). Our studies of the fungal and microbial communities in oak forests along the study transect found that the urban forests exhibited reduced fungal biomass and microarthropod densities in relation to the rural stands. These results support the commonly held belief that urban forests have depauperate communities because of anthropogenic stress (Goudie, 1990).

Unlike the population and community effects, the ecosystem effects along the urban-rural gradient proved to be more complex and contrary to commonly held ecological beliefs. Litter decomposition and nitrification rates were higher in urban forests than in rural forests even though they had poorer leaf litter quality. The lower quality litter, in part, explains the lower nitrogen-mineralization rates, lower methane consumption, lower labile soil carbon pools, and higher total passive soil

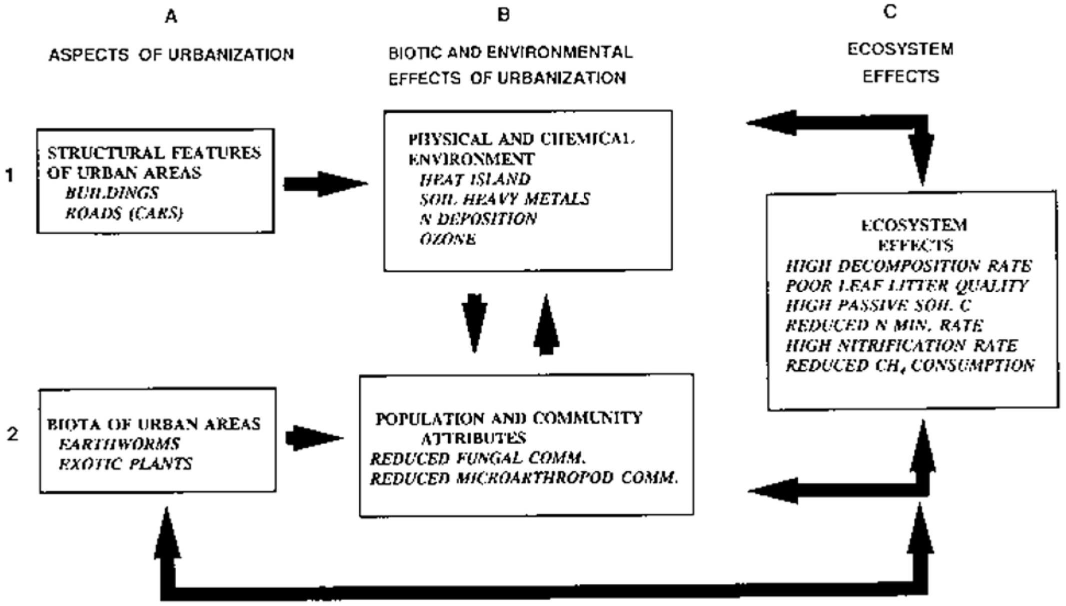

Fig. 3 The composite model of the effects of urbanization in ecological phenomena listing critical factors for each component determined in the study of a 140 × 20 km urban-rural gradient running from the New York City urban core to rural Litchfield County, Connecticut. Note the addition of the strong interaction between the biota of urban areas and ecosystem effects components of the model due to the activities of earthworms in the urban forests

carbon pools in urban forests in relation to the rural forests. The higher average temperature at the urban end of the transect may, in part, explain the increased rates in ecosystem processes in the urban forests. The key to understanding nutrient cycling in the urban forests proved to be the large densities and biomass of non-native earthworms at the urban end of the gradient which falls in the 'aspects of urbanization' component of our model (Fig. 3).

It has long been recognized that earthworms can greatly increase the loss of surface litter (Raw, 1962; Lee, 1985; Lavelle, 1988). Satchell (1976) concluded that the amount of organic matter consumed by earthworms was limited by the amount available rather than by their capacity to ingest it. In no-tillage agroecosystems in Georgia, Parmelee *et al.* (1990) reported that earthworms increased organic matter loss by 45%, and on a rich mull site in Sweden, earthworms were associated with higher decomposition rates of beech litter compared with less fertile soils (Staaf, 1987).

Earthworms can also directly affect available nitrogen and nitrogen-mineralization rates. Direct nitrogen flux, as estimated by secondary production, can be considerable. For example, Parmelee and Crossley (1988) calculated an annual nitrogen flux of 63 kg/ha in a no-tillage agroecosystem. Earthworms ingest organic material of relatively wide C:N ratios and convert it to earthworm tissue of lower C:N ratio (Syers and Springett, 1984). Nitrogen is then returned to the soil in dead tissue, urine, and mucoproteins. Satchell (1967) estimated that a minimum of 70% of the nitrogen in dead earthworm tissue was mineralized in 10–20 days. Annual urine excretion for lumbricoid populations has been estimated to be 18.5 kg/ha (Lee, 1982) and similar inputs have been estimated for mucoproteins (Dash and Patra, 1979). Whether or not earthworms increase system loss of nitrogen is not clear. Earthworms increased the amount of ammonia and nitrate in leachate from forest litter (Anderson and Ineson, 1984) and the percentage of inorganic nitrogen in leachate from grassland soils (James and Seastedt, 1986).

In addition to direct effects of earthworms on decomposition and nitrogen-mineralization, earthworms may also affect these processes by altering the structure and function of the decomposer food web. This research is largely based on studies of earthworm casts. Casts generally have higher moisture, carbon and nitrogen contents, and often a higher C:N ratio than surrounding soil, and thus provide a favorable habitat for increased microbial activity (Parle, 1963; Lee, 1985; Shaw and Pawluk, 1986; Scheu, 1987). Classic mull vs. mor comparisons have found mull soils to be dominated by earthworm activity, lower fungal and higher bacterial densities, and lower microfaunal populations. Macroinvertebrates may also shift the bacterial:fungal ratio to favor bacteria (Anderson, 1988). It has been hypothesized that shifting to a bacterially based food web can lead to greater decomposition and nitrogen-mineralization rates (Hendrix *et al.*, 1986). Earthworms have also been implicated in altering the structure of collembolan communities (Marinissen and Bok, 1988) and decreasing nematode populations (Yeates, 1981). These observations are consistent with the lower fungal hyphae and nematode and microarthropod populations we have observed in our urban forests.

Conclusion

Our studies suggest a potential cause and effect relationship between the physical and chemical environment along the gradient and changes in oak forest community structure and ecosystem processes. Forests at the urban end of the gradient exhibit reduced fungal and microarthropod populations and poorer leaf litter quality than the more rural forests. But, the potential negative effect of these conditions on ecosystem processes such as decomposition and nitrogen-cycling in the urban forests appears to be ameliorated by two other anthropogenic causes: increased average temperatures caused by the heat island effect and the introduction and successful colonization of earthworms in the urban forests. Forests at the urban end of the transect, in fact, exhibit faster litter decomposition and nitrification rates than the rural forests. Our current and planned research has focused on experimental studies designed to test the hypotheses generated by the results of our work. All future studies of urban-rural gradients should be coupled whenever possible with experimental studies to test the hypotheses suggested by gradient analyses.

The documentation of environmental changes and the community and ecosystem response of forests along an urban-rural gradient provide a new template for ecological research. North American ecologists have only rarely studied the structure and function of populations, communities, and ecosystems under varying and known degrees of human population densities and their associated effects. The study of ecological systems along urban-rural gradients could readily expand to discover new patterns and interactions at genetic, physiological, population, community, ecosystem, and landscape levels. Furthermore, the linkages among interactions at various levels might well be sensitive to position along the gradient. Because the combination of stresses and disturbances is new and often extreme at certain ranges of the gradient, the potential to exploit the urban rural gradient as an unplanned, but profound experimental treatment is great. It provides a new, but widespread substrate for ecological study, and a potential interface for ecology with the study of human societies. In the face of global environmental change, it is critical to understand such an interface in order to develop predictions about how these important areas may change in the future.

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