
Vegetation composition and structure of forest patches along urban-rural gradients

WAYNE C. ZIPPERER AND GLENN R. GUNTENSPERGEN

Introduction

The urban landscape is highly altered by human activities and is a mosaic of different land covers and land uses. Imbedded in this are forest patches of different origins (Zipperer *et al.*, 1997). How these patches influence and are influenced by the urban landscape is of ecological importance when managing the urban forest for ecosystem goods and services.

To evaluate how forests respond to altered environmental conditions of urban landscapes, McDonnell and Pickett (1990) proposed an urban-to-rural gradient approach. The approach builds on an established ecological methodology, gradient analysis, to evaluate species response to changes in environmental conditions (Whittaker, 1967; Pickett *et al.*, Chapter 3). Two basic categories of gradient analyses exist - direct and indirect. Simplistically, direct gradient analysis is typically employed when a single factor is used or the underlying environmental factors are organised linearly, whereas indirect gradient analysis is used when the multiple interacting factors and the environmental factors are not organised linearly across a landscape or in a regular pattern (Ter Braak and Prentice, 1988). Other approaches exist for studying the response of ecosystems to altered environmental conditions in urban environments, such as biotope mapping (Breuste, Chapter 21) and patch dynamic approaches (Nilon, Chapter 10).

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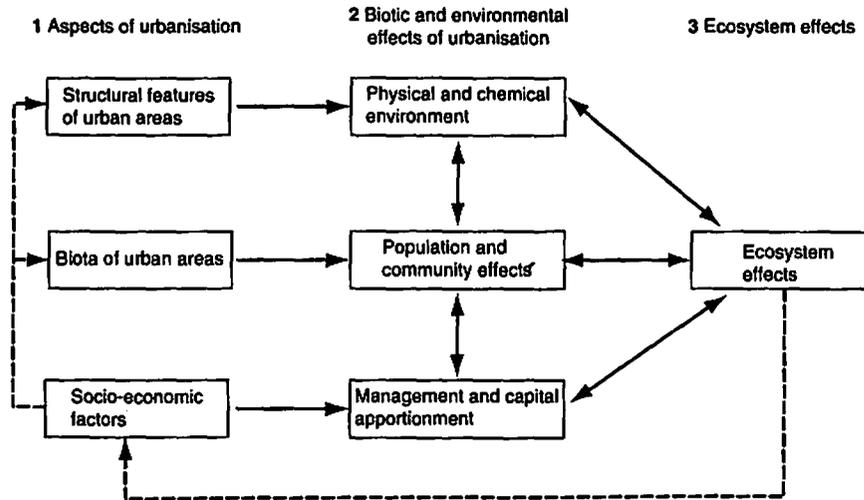


Fig. 17.1. A composite model showing the effect of urbanisation on ecological components. The solid lines represent the original model proposed by McDonnell and Pickett (1990). The dash lines are feedback loops to link ecosystem effects (altered goods and services) back to socio-economic components.

Unlike many environmental gradients where environmental factors (e.g. in temperature, moisture, elevation) change linearly, urbanisation does not change linearly (high to low) across a metropolitan region (McDonnell *et al.*, 1993). Consequently, urbanisation actually is best represented by indirect gradient analysis, where population, community and ecosystem responses are analysed and urban gradients are identified.

The urban-rural gradient is not a new idea and has been used by individuals prior to McDonnell and Pickett (1990) (see Airola and Buchholz, 1984; Dorney *et al.*, 1984; Moran, 1984). But McDonnell and Pickett (1990) moved the science from merely describing species changes along an urban continuum to framing how ecosystems - their structure, function and change - are altered by urbanisation and the consequences to society (Niemelä *et al.*, Chapter 2; Pickett *et al.*, Chapter 3; Natuhara and Hashimoto, Chapter 12; Carreiro *et al.*, Chapter 19; Pouyat *et al.*, Chapter 20). To portray the effect of urbanisation on ecosystems, they proposed a composite model with three components: (1) aspects of urbanisation; (2) biotic and environmental effects of urbanisation; and (3) ecosystem effects (Fig. 17.1). The model emphasises the effect of the urban landscape on ecosystem structure and function without any ecological feedback on the social system (Zipperer *et al.*, 1997). See Pickett *et al.* (Chapter 3) for more discussion of the feedbacks between ecological and social systems.

A second type of urban-rural gradient is proposed by Porter *et al.* (2001). Rather than evaluating a specific ecosystem in different urban contexts, they

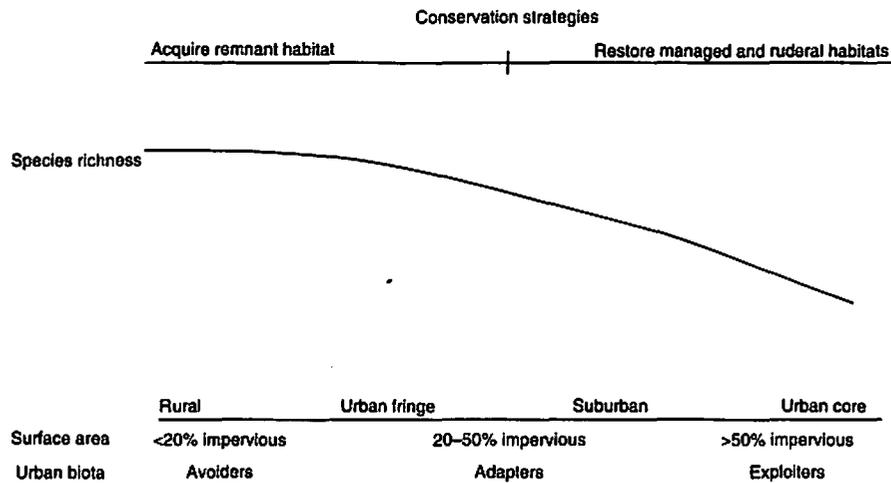


Fig. 17.2. A graphic representation of changes in impervious surface, species richness, species composition and conservation strategies along urban-rural gradients as proposed by McKinney (2002).

propose to compare different land-use cover types to a natural ecosystem. For example, Blair (1996) examined how bird diversity varied from a forested patch to various urban land-use types including residential, recreational and commercial (see also Catterall, Chapter 8). The analysis provides insights into species responses to different land-cover types. Yang and Zhou (Chapter 16) and McDonnell and Hahs (Chapter 5) discuss other remote sensing and GIS variables that can be effectively used to define urban-rural gradients.

McKinney (2002) reviewed the current literature on how urbanisation alters ecosystems and offered conservation strategies for managing ecosystems and educating the public about the importance of maintaining ecosystems in urban and urbanising landscapes. From the review, he identified several general patterns from rural to urban (Fig. 17.2): impervious surface increases, native species richness declines, species composition shifts from interior to ruderal species, and conservation strategies shift from acquiring remnant patches to restoring managed and ruderal habitats (McKinney, 2002). These observations often were derived from studies examining species responses to different land covers rather than a specific ecosystem in different urban contexts.

In this chapter, we will use McDonnell and Pickett's (1990) composite model of urban effects on ecosystems and McKinney's (2002) descriptive model of species and management responses to urbanisation to examine patterns of species composition and structure in remnant and reforested forest patches, and remnant forest productivity, along urban-rural gradients in Maryland, New Jersey, New York and Wisconsin (Levenson, 1981; Airola and Buchholz, 1984;

Table 17.1. General descriptions of urban-rural gradients used to compare vegetation composition and structure.

Milwaukee	24 remnant upland forest patches (Guntenspergen and Levenson, 1997). Patches were dominated by sugar maple (<i>Acer saccharum</i>) and occurred on soils with similar characteristics. All patches had mature forest edges and were devoid of recent disturbances such as grazing, cutting, fire and windthrow. Patches ranged from 0.59 to 21.0 ha.
Palisade	Only five forested patches along the Palisades escarpment in New Jersey (Airola and Buchholz, 1984). Patches were remnant forests. Three occurred within the Palisades Interstate Park and showed little signs of disturbance. The other two patches were on unprotected urban sites. Patch sizes ranged from 2.5 to 16 ha.
Baltimore	45 remnant upland forest patches (W. C. Zipperer, in preparation) along an urban-rural gradient in the Gwynns Falls watershed. Patches were >5 ha in size. All patches had mature forest edges and were devoid of recent disturbances such as grazing, cutting, fire and windthrow.
Syracuse	Both remnant (44) and reforested (52) upland forest patches (Zipperer, 2002). All sites had established canopies and did not show any signs of recent large-scale disturbances. Patch sizes ranged from 0.25 to 85 ha.

Kostel-Hughes, 1995; Guntenspergen and Levenson, 1997; Kostel-Hughes *et al.*, 1998a; Zipperer, 2002; Table 17.1). Although urbanisation is best represented by indirect gradient analysis, in this analysis we used the direct gradient as outlined by the researchers in each of the mentioned studies because indirect gradient information was not available for all of the studies.

Aspects of urbanisation

In their composite model, McDonnell and Pickett (1990) identified three elements - structural features, biota and socio-economic factors of urban areas (Fig. 17.1) - as the principal drivers influencing ecosystem structure and function. Here, we specifically examine how structural attributes define the urban landscape and their effect on forested ecosystems.

Structural features

European settlement of North America fragmented large tracts of forest into smaller forest remnants as forest lands were cleared for agriculture (e.g. Curtis and McIntosh, 1951), altering external allogenic and autogenic processes (Saunders *et al.*, 1991). As landscapes became more urbanised, landscape context changed, and allogenic and autogenic processes changed as anthropogenic disturbances (e.g. trampling and arson) supplanted natural processes and disturbances

such as fire (Parker and Pickett, 1997). Further, with the shifts in landscape context, the functional aspect of the edge changed (see Cadenasso *et al.*, 1997). The conversion of non-urban land to urban land use has been extensively studied. For example, Godron and Forman (1983) examined landscape modifications by humans and identified several effects including linearisation of feature, reduction of patch size, increase in patch isolation and fragmentation, and a shift from interior to edge habitat. It is not the purpose of this section to review the literature on conversions to urban land use, but instead we use three studies – Zipperer *et al.* (1990), Medley *et al.* (1995) and Luck and Wu (2002) – to characterise general patterns of structural features observed along urban–rural gradients. Zipperer *et al.* (1990) conducted a spatio-temporal analysis of forest patches in five different landscape types – forest, forest+agriculture, forest+urban, agriculture, agricultural+urban, and urban. The dominant or co-dominant land use or cover defined a landscape. His analysis showed a similar pattern to that seen by Godron and Forman (1983), but it also showed that even though a landscape was urban (dominant land use), fragmentation and deforestation continued to reduce patch size and eliminate patches, increasing the isolation of the remaining forest patches.

Medley *et al.* (1995) quantified the New York urban–rural gradient by using a set of landscape parameters along a linear transect from highly urbanised New York City to rural Litchfield County, Connecticut. Social parameters included population density, traffic volume, road density and percentage of land use (residential, urban-mixed, forest, agriculture, wetland, abandoned land and water). Forest patch attributes included mean patch size, patch density, and percentage of total forest edge adjacent to urban-mix and residential land uses. Although the results were similar to the previous study, Medley *et al.* (1995) also revealed that disturbances associated with urbanisation show a complex spatial pattern not clearly related to a linear distance from urban to rural.

Looking more closely at patch dynamics and applying different patch metrics to an urban landscape, Luck and Wu (2002) conducted a detailed patch analysis in the urban and urbanising landscapes of the Phoenix Metropolitan area. They observed patterns for desert vegetation similar to those described by Godron and Forman (1983), Zipperer (1990) and Medley *et al.* (1995) – declines in size and total number of patches and increased isolation with an increase in urban land use. They also reported that urban landscapes can be quantified using known patch metrics, and land-use types did differ to some extent with regard to these metrics (Luck and Wu, 2002). Land-use types, however, did not show a distinct landscape signature but rather a 'landscape pattern profile'. Further, their analyses supported McDonnell and Pickett's (1990) hypothesis that a gradient analysis using patch metrics can help to quantify complex urban landscapes and subsequently relate attributes to ecosystem patterns and processes.

Biota of urban areas

Human activities lead to a high diversity of non-native species in urban landscapes (Kowarik, 1990; Porter *et al.*, 2001; Catterall, Chapter 8; Nilon, Chapter 10; van der Ree, Chapter 11; Natuhara and Hashimoto, Chapter 12; McIntyre and Rango, Chapter 14 and Meurk *et al.*, Chapter 18). Although most species introductions do not affect ecosystems, about 5% can become invasive and affect ecosystem structure and function (Reichard and White, 2001). Ecologists are just beginning to understand how these non-native species are altering urban forest patches. For example, exotic earthworms alter denitrification in urban forest soils (Steinberg *et al.*, 1997). Similarly, Ehrenfeld (2003) reports that non-native species increase biomass and net primary production, increase nitrogen (N) availability, alter nitrogen fixation rates and produce more litter than co-occurring native species. Non-native species also compete with native species for available growing space and nutrients. Understanding how non-native species alter community and ecosystem dynamics is a central theme for today's urban ecologists.

Socio-economic factors

In addition to these structural and biotic effects, urban woodlands also are strongly influenced by socio-economic factors and processes (Grove and Burch, 1997). Collectively, these factors and processes can be defined as socio-genic, and are often accounted for in ecological studies by land-use patterns. However, a land-use classification does not capture the wealth of social heterogeneity within a land use and how that heterogeneity influences the movement of energy, species and materials (Machlis *et al.*, 1997). Several studies indicate the importance of accounting for social heterogeneity with respect to species availability and performance (see Whitney and Adams, 1980; Richards *et al.*, 1984). To account for sociogenic processes, Grove and Burch (1997) recommend defining social areas as patches based on socio-economic attributes and capital, such as ethnicity, education, home ownership and income. These socio-economic patches are then overlaid on ecological patches (e.g. forest patches) to examine interactions and relationships between social and ecological patterns and processes. In addition, the patch approach enables hierarchical analyses to examine how the different social attributes influence ecological processes at different scales (Pickett *et al.*, 1997b).

Alberti *et al.* (2003) present a conceptual framework that differs from the patch approach of Pickett *et al.* (1997b). The framework accounts not only for the interactions between human and biophysical patterns and processes, but also the feedbacks from these interactions. Regardless of the approach, both Pickett *et al.* (1997b) and Alberti *et al.* (2003) recognise the importance of social context

within an urban landscape and its influence on ecosystems. The urban-rural gradient can be used to assess how different social contexts influence ecosystem structure and function, and how different ecosystems can affect social contexts (Pickett *et al.*, Chapter 3).

Biotic and environmental effects

Physical and chemical

Environmentally, urban landscapes are highly altered when compared with natural systems. For example, a comparison of urban and rural forest soils shows that urban forest soils have a higher organic content (i.e. decomposed material) in the O₂ horizon, possibly the result of earthworm activity (Pouyat *et al.*, 1995a; Steinberg *et al.*, 1997), a lower litter depth (Kostel-Hughes *et al.*, 1998a) and, in some areas, greater bulk density from compaction. Internal functions of urban woodlands also differ from those in rural woodlands. Urban woodlands have higher rates of decomposition, nitrification and seed predation (Nilon, 1996; Pouyat *et al.*, 1996; Carreiro *et al.*, 1999; Zhu and Carreiro, 1999; Carreiro *et al.*, Chapter 19 and Pouyat *et al.*, Chapter 20), and possibly have lower soil moisture (White and McDonnell, 1988). Decomposition, nitrification and soil moisture influence the concentration and type of nutrients available for plant growth. Higher rates of seed predation may influence successional development of the site. And because of a concentration of human activities (e.g. hiking and biking), more soil erosion and reduced infiltration from compaction occur in urban woodlands than in rural woodlands. In addition to these direct effects, urbanisation affects the woodland indirectly by altering the disturbance regime; increasing ambient temperatures (urban heat island); increasing pollution deposition of heavy metals, nitrogen, calcium and manganese; modifying hydrology; and introducing non-native species (Pouyat and McDonnell, 1991; Lovett *et al.*, 2000; Reichard and White, 2001). A more detailed evaluation of environmental effects is presented by Carreiro *et al.* (Chapter 19) and Pouyat *et al.* (Chapter 20).

Population and community effects

Changes in the physical, biotic and structural attributes along urban-rural gradients affect species composition and structure in vegetation. McKinney (2002) describes a shift in composition from a dominance of interior species to a dominance of ruderal species as one moves from rural to urban sites. This pattern seems to hold true for both flora and faunal communities. For example, Porter *et al.* (2001) observed no changes in structural attributes of woody vegetation (>3 cm diameter at breast height, dbh) across six land-use types (forest

preserve, recreational, golf course, residential, apartments and industrial), but did observe changes in species richness. The richness analyses did not show a decline in native species richness, but did show an increase in non-native species richness, principally from ornamental planting and gardens. The occurrence of native species across these land-cover types was attributed to planting of native species and to remnant individuals (e.g. McBride and Jacobs, 1976). Porter *et al.* (2001), however, did observe a greater faunal change across the land-cover types. The social context of each land-cover type significantly influenced flora and fauna (see also Meurk *et al.*, Chapter 18; Florgård, Chapter 22; Ignatieva and Stewart, Chapter 23). And, although this and similar studies (Blair, 1996) identify changes associated with urbanisation, these changes are based on changing land-use types. We will show that comparisons of forests along urban-rural gradients also show shifts in species composition and structure.

Remnant forests

To evaluate how species composition and structure varied across an urban-rural gradient, we separated forest structure into three categories of vertical structure: canopy, shrub/sapling and seedling. For upland remnant forests, non-native species richness for canopy, shrub/sapling, and seedling strata increased from rural to urban, regardless of patch origin (Tables 17.2, 17.3 and 17.4). However, two distinct patterns of native species richness were observed. Along the New Jersey Palisade gradient, native species richness declined in the canopy, shrub/sapling and seedling strata (Airola and Buchholz, 1984). By comparison, native species richness for each stratum was unchanged for the Milwaukee (Levenson, 1981; Ranney *et al.*, 1981; Guntenspergen and Levenson, 1997), Baltimore and Syracuse remnant forest patches (Zipperer, 2002; W.C. Zipperer,

Table 17.2. Changes in native and non-native species richness in the canopy stratum for different urban-rural gradients.

Gradient	Native species	Non-native species
Palisade	↓	↑
Milwaukee	↔	↑
Syracuse: Remnant	↔	↑
Syracuse: Reforested	↔	↑
Baltimore: Remnant	↔	↑

Notes:

↑: increased from rural to urban

↓: decreased from rural to urban

↔: no change

Table 17.3. Changes in native and non-species richness in the sapling/shrub stratum for different urban-rural gradients.

Gradient	Native species	Non-native species
Palisade	↓	↑
Milwaukee	↔	↑
Syracuse: Remnant	↔	↑
Syracuse: Reforested	↓	↑
Baltimore: Remnant	↔	↑

Notes:

↑: increased from rural to urban

↓: decreased from rural to urban

↔: no change

Table 17.4. Changes in native and non-species richness in the seedling stratum for different urban-rural gradients.

Gradient	Native species	Non-native species
Palisade	↓	↑
Milwaukee	↔	↑
Syracuse: Remnant	↔	↑
Syracuse: Reforested	↓	↑
Baltimore: Remnant	↔	↑

Notes:

↑: increased from rural to urban

↓: decreased from rural to urban

↔: no change

unpublished data). This difference may be related to sampling intensity and patch disturbance regime. Airola and Buchholz (1984) sampled only two forest patches in the urban landscape, so they did not have sufficient data to give an adequate representation of forest conditions. In addition, the Palisade gradient did not control for disturbance. In the urban forest patches, canopy cover was not continuous and tree density was much lower than in the undisturbed sites along the Palisade. For the Syracuse, Baltimore and Milwaukee gradients, canopy cover was maintained and disturbances were limited to small-scale events (Sharpe *et al.*, 1986; Zipperer, 2002).

Structurally, with the exception of Palisade, each gradient showed an increase in tree stem density. All the gradient studies showed an increase in shrub/sapling

Table 17.5. Changes in structural characteristics for different urban-rural gradients.

Gradient	Tree density	Shrub/sapling density	Seedling density
Palisade	↓	↑	↓
Milwaukee			↓
Syracuse: Remnant	↑	↑	↓
Syracuse: Reforested	↔	↑	↓
Baltimore: Remnant	↑	↑	↓

Notes:

↑: increased from rural to urban

↓: decreased from rural to urban

↔: no change

density, but also a decline in seedling density. In the New Jersey gradient, tree density declined. Unfortunately, long-term monitoring of species composition and structure of forest patches along an urban-rural gradient is lacking. However, a number of studies of temporal changes in structure and composition of forest patches in the urban landscape have been conducted (e.g. Rudnický and McDonnell, 1989; Botkin, 1990). In each case, we do not see a loss of native species, but rather a shift in species importance and an increase in non-natives. In general, the structure shifted from long-lived, shade-tolerant species (*Acer saccharum*, *Quercus* spp. and *Fagus grandifolia*) to short-lived, shade-intolerant species (*Liriodendron tulipifera*, *Prunus serotina* and *A. rubrum*).

Reforested patches

Unlike the studies examining remnant forest patches along urban-rural gradients, analysis of reforested patches is limited (Zipperer, 2002), so the pattern that we observed, a decrease in native species richness but an increase in non-native species across all structural categories (Tables 17.2, 17.3 and 17.4), needs to be verified for other locations. Reforested patches in Syracuse, New York, were dominated by non-native species (Zipperer, 2002), and those species differ from the dominant species occurring in rural reforested patches. In the urban landscape, *Acer negundo*, *A. platanoides* and *Fagus pennsylvanica* are the dominant tree species. In the rural sites, *A. rubrum* and *Fraxinus americana* are the dominant species. Structurally, sites are similar in tree density, but differ with respect to shrub/sapling density and seedling density (Table 17.5). Rural sites had lower shrub/sapling densities but higher seedling densities. A number of factors could cause these differences including site disturbances, species availability and altered site conditions. Additional research, however, is needed

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to identify how these factors influence the observed species distribution and structural characteristics.

Ecosystem effects

The analysis of urbanisation on ecosystem function has focused principally on soil processes (see McDonnell *et al.*, 1997) rather than forest processes, such as productivity. Nevertheless, the soil studies have pointed out two factors that can significantly affect productivity: warmer soil temperatures and higher levels of available nitrogen. Analysis of phenological differences between urban and rural areas also indicates that the growing season was 7.6 days longer in urban than in rural broad-leaf deciduous areas in the eastern United States (White *et al.*, 2002). Coupling this observation with an increase in carbon dioxide in urban landscapes (Idso *et al.*, 2001), one would predict a higher rate of productivity in urban areas than rural areas. Using eastern cottonwood (*Populus deltoides*) clones planted along an urban-rural gradient in the New York metropolitan area, Gregg *et al.* (2003) showed higher productivity rates for the urban plantings. These higher rates, however, were not attributed to higher urban temperatures and CO₂ concentration but rather to higher levels of ozone in rural areas, which reduced productivity.

A comparison of leaf weight for the permanent plots established within the Gwynns Falls watershed in Maryland and a forested reference site in Oregon Ridge State Park located north of the watershed (part of the Baltimore Long-Term Ecological Research Project) showed that rural sites had a greater mass per leaf area suggesting thicker leaves (W. C. Zipperer, unpublished data). Carreiro *et al.* (1999) also observed the same pattern for oak forest patches along a New York urban-rural gradient. Ozone is known to affect leaf thickness (Berish *et al.*, 1998). The observed differences in leaf weight per area for both Maryland and New York gradients suggest that some environmental factor is influencing stand growth, possibly ozone as hypothesised by Gregg *et al.* (2003).

No differences in the mean annual growth increment of trees in remnant stands greater than five hectares in the Gwynns Falls watershed were observed between the upper section (rural) and the lower section (urban). No differences in tree growth were observed between rural and urban areas. Regardless of tree age, the middle or 'suburban' section had the lowest mean annual increment. These observations differ from what would be predicted from Gregg *et al.* (2003). The lower or urban section should have the highest productivity. The mean annual increment analysis did not involve saplings. A more detailed analysis of individuals from each stratum - tree, shrub/sapling, and seedling/herbaceous - is needed to understand the complexity of forest productivity along an urban-rural gradient.

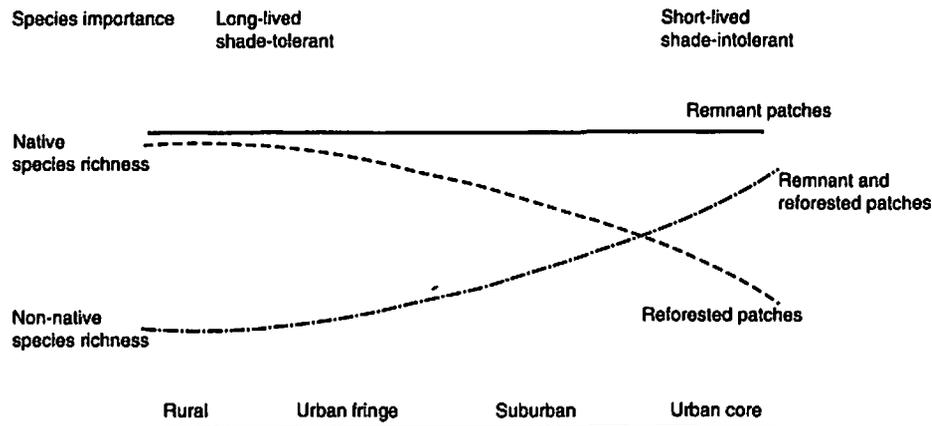


Fig. 17.3. A modification of McKinney's (2002) model for changes along urban-rural gradients to illustrate changes in species richness and importance observed for remnant and reforested patches.

Revised urban-rural model

By comparing only forest patches with similar disturbance regimes and origin along urban-rural gradients, we observed that native species richness remains relatively constant but non-native species richness increases. As the disturbance regime changes, native species richness declines (Airola and Buchholz, 1984; Zipperer, 2002). This decline, however, needs to be substantiated with additional studies. Regardless of the disturbance regime, non-native species increased in both remnant and reforested patches. Seedling density declined with an increase in urban land use. In reforested sites, native species richness also declined, and unlike their rural counterparts, urban reforested patches were often dominated by non-native species.

Even with similar disturbance regimes and compositions, upland remnant forest patches may be shifting in species importance as shade-tolerant species give way to shade-intolerant species. This pattern is suggested by McKinney (2002) as a shift from interior to ruderal species. Structurally, the forest is composed of a higher density of smaller diameter trees. More studies are needed to understand how the environment of an urban landscape affects tree growth and patch productivity.

We propose the following modifications to McKinney's (2002) model (Fig. 17.3). First, no single model can capture the variation observed in urban landscapes because of differences in site legacies and disturbance regimes. Second, for woody plant species, species richness needs to be separated into native and non-native categories to capture changes along the gradient. Finally, the use of

species importance, rather than interior and ruderal categories, may capture potential changes in stand structure.

These modifications do not suggest that McKinney's (2002) model is wrong or incomplete; to the contrary, we are adding another dimension to our understanding of how the urban landscape affects flora and fauna. Actually, how one views the urban landscape depends on perspective. Looking across similar land-cover types in different urban contexts will yield different patterns than examining how different land covers differ in urban landscapes. Because of the social, physical and ecological complexities in urban landscapes, we need to initiate detailed studies that examine these differences to better understand urban effects on ecosystem patterns and processes.

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