Landscape Ecol (2008) 23:1143–1155
DOI 10.1007/s10980-008-9253-4

RESEARCH ARTICLE

The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions

Mark J. McDonnell · Amy K. Hahs

Received: 30 July 2007 / Accepted: 12 August 2008 / Published online: 28 August 2008

Abstract Over the past decade, the urban–rural gradient approach has been effectively used to study the ecology of cities and towns around the world. These studies have focused on understanding the distribution of plants and animals as well as ecosystem processes along gradients of urbanization that run from densely urbanized inner city to more rural exurban environments. We reviewed 300 papers investigating urbanization gradients that were published in peer-reviewed journals between 1990 and May 2007. Sixty-three percent of the papers investigated the distribution of organisms along urbanization gradients. Only five papers addressed the measures used to quantify the urbanization gradient itself. Within the papers addressing the distribution of organisms, 49% investigated the responses of birds to urbanization gradients, and <10% of the papers investigated more cryptic organisms. Most of these studies utilized a variety of broad measures of urbanization, but future advances in the field will require the development of some standardized broad measures to facilitate comparisons between cities. More specific measures of urbanization can be used to gain a mechanistic understanding of species and ecosystem responses to urbanization gradients. While the gradient approach has made a significant contribution to our understanding of the ecology of cities and towns, there is now a need to address our current knowledge gaps so that the field can reach its full potential. We present two examples of research questions that demonstrate how we can enhance our understanding of urbanization gradients, and the ecological knowledge that we can obtain from them.

Keywords Urban–rural gradients · Biodiversity · Landscape ecology · Urbanization · Characterizing urban landscapes · Melbourne, Australia · Auckland, New Zealand · Tree species richness

M. J. McDonnell (✉) · A. K. Hahs
Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne, c/o School of Botany, University of Melbourne, Melbourne, VIC 3010, Australia
e-mail: markmc@unimelb.edu.au

A. K. Hahs
e-mail: hahsa@unimelb.edu.au

Introduction

The ever increasing human population is driving the expansion and creation of cities and towns worldwide. The process of urbanization changes the landscape, generating more impervious surfaces and artificial structures (Gilbert 1989; Collins et al. 2000; McKinney 2002). It also results in high densities of people, domestic plants and animals, while also altering the flux of nutrients, organisms, energy and water within and between landscapes (McDonnell and Pickett 1990; Niemelä 1999; Grimm et al. 2000; Pickett et al. 2001). Consequently, there is a tremendous call for more ecological information in urban and exurban environments by natural resource managers, planners, conservationists, scientists, and professionals associated with human health to inform planning and management decisions required to create more sustainable cities.

In the early 1990s, McDonnell and Pickett (1990) proposed the gradient approach as a useful method for studying the ecology of cities and towns. This approach provides a useful tool for developing a greater understanding of the interactions between urban development and the structure and function of ecological and social systems (Alberti et al. 2001; Alberti 2008). The importance of quantifying urbanization gradients as discussed by McIntyre et al. (2000) was an important step for it allows for comparisons between different gradients within and between cities. This was also a significant step forward for researchers, planners and managers because it allowed for the amalgamation of ecological and social science information (Theobald 2004).

We are currently at an appropriate stage in the development and use of the gradient approach to assess what we have learned, and what improvements can be made in the future to achieve better research, management and conservation outcomes. The objectives of this paper are to: (1) review the concept of urbanization gradients; (2) discuss the measures used to characterize the gradients; (3) briefly assess the current status of our understanding of the ecology of cities and towns that has been achieved using the gradient approach and (4) describe future research directions.

The concept of urbanization gradients

The concept of urbanization gradients is based on the well-established application of gradient analysis tools to understand the ecology and distribution of plants and animals in response to physical, chemical, ecological and micro-climatic changes in the environment (ter Braak and Prentice 1988). One of the most commonly cited examples of the effective use of gradient analysis techniques in ecology is the study of vegetation along elevation gradients (Whittaker 1967). Elevation is an indirect gradient because the height of a mountain is only a surrogate or dummy variable that is correlated with changes in a variety of environmental variables including temperature, humidity, rainfall and soil depth. In addition, gradients of elevation are not always linear as mountains commonly have undulating topography resulting in non-linear changes in physical and micro-climate conditions (i.e., they form a complex gradient). In contrast, soil moisture gradients surrounding a bog or fen represent direct gradients, because the organisms are responding to the moisture levels in the soil. Such gradients are also commonly linear (simple) and easily studied using transects. Most ecological gradients are complex and involve several contrasting variables. Thus, a hierarchical analytical approach which acknowledges the nested nature of ecological systems by addressing different spatial and temporal scales is necessary to investigate the relative importance of potential causal factors and the ecological responses of species, communities and ecosystems to these gradients (Allen and Wyleto 1983). This is especially important when studying anthropogenic gradients because other non-anthropogenic factors such as climate, habitat availability, and species interactions are equally important to understanding the abundance and distribution of organisms and ecosystem processes (Allen and O'Connor 2000).

Urbanization gradients are essentially anthropogenic gradients produced as a consequence of the creation of human settlements. The major environmental changes that occur during the process of urbanization include: (1) creation of new land-cover; (2) alterations to the chemical and physical environment; (3) the creation of new assemblages of organisms and (4) alterations to disturbance regimes (Sukopp 1998; Kinzig and Grove 2001). Gradients of urbanization, similar to elevation, are indirect and complex (McDonnell et al. 1993). The framework proposed by McDonnell and Pickett (1990) provided a hierarchical approach to the study of the multiple causal factors and responses related to environmental changes associated with urbanization. It is important to note that there are other ecological frameworks such as patch dynamics (Pickett et al. 2001), the classic ecosystem approach (Zipperer et al. 2000), meta-population dynamics (Marzluff et al. 2001), mechanistic studies (Shochat et al. 2006) and the human ecosystem model (Pickett and Cadenasso 2006) that are also useful in understanding the ecology of urbanizing landscapes.

Typically, the most intense 'urban' environmental conditions occur in the older, more human-modified center of cities, with decreasing 'urban' effects further away from the city centers. Using an analogy to elevation gradients, the intensely developed city centers would be the mountain peaks with the harshest conditions present on the gradient, whereas the less intensely developed suburbs and peri-urban areas would be equivalent to the slopes and valley bottoms. Due to the unique combinations of social, economic and environmental drivers that underlie the rate of development of every city, it is important to note that cities would not form a single 'mountain' but instead would be more accurately described as a 'mountain range' (i.e., more polycentric than mono-centric). Thus, in building cities and towns, humans create a diverse mosaic of environmental conditions that can be effectively studied using gradient analysis techniques. The gradient approach used needs to be able to quantify not only the 'mountain' peaks but also the slopes and valleys within these 'mountain ranges'.

Measures used to characterize urbanization gradients

In the past, urbanization gradient studies have been criticized for presenting gradients that have been too simplistic (Alberti et al. 2001; McKinney 2006; Alberti 2008). This has largely been due to the prevalence of the transect approach to represent the urbanization gradient (McDonnell et al. 1993, 1997; Luck and Wu 2002). As our understanding of urbanization has developed, the importance of capturing the characteristics of the landscape at different locations along the gradient has come into focus (McIntyre et al. 2000). The increased uptake of geographic information systems and the greater availability of satellite imagery has also played a role in moving away from the use of transects to define gradients, to using direct measures of urbanization at a location to characterize the local landscape context. However, we need to improve our understanding of the measures used to define the gradient, as well as those used for the response variables, as the selection of specific measures can influence the findings of the study (Hahs and McDonnell 2006).

Gradients can be defined with differing levels of precision. Broad measures of urbanization are equivalent to the elevation gradient for mountains; they can be easily measured but are likely to capture a complex range of conditions. Examples of broad measures of urbanization include: density of people or dwellings, or the proportion of built surfaces. Specific measures of urbanization are equivalent to the temperature or soil moisture measures of mountain gradients. They provide a more precise measure of the characteristics of the urban area that are likely to have a direct influence on the ecological response. For example, Jerzak (2001) found a correlation between the number of garbage bins per km^2 and the density of breeding pairs of black-billed magpies in Zielona Gora, Poland. The trade-offs between broad and specific measures of urbanization relate to the resources required to calculate the measure and their applicability in studies examining different ecological responses. Broad measures of urbanization are generally calculated using existing data sets and can therefore be obtained at relatively little cost, and generally are available for many different cities. Specific measures of urbanization may require the collection of additional data, or compilation of data from a number of sources, which is likely to have a higher associated cost. Also, specific measures for one study may not be the most relevant measure for another study. For example, garbage bins may influence bird densities, but they are less informative for studies investigating frog diversity.

The distinction between broad and specific measures of urbanization is an important one, as both categories can contribute to the study of urbanization gradients. The use of broad measures of urbanization has an important role to play in advancing our understanding of ecology in and of cities for two reasons. Firstly, they provide a general definition of the gradient that can be used to establish some basic ecological research in urban areas where previous information is absent. Secondly, they provide a common element that allows for a greater integration between studies conducted on different systems, or at different places in time or space (McIntyre et al. 2000). An example of using the urbanization gradient approach at a global scale is the Globenet project which aims at gaining a general understanding of the biotic consequences of urbanization by using the same taxonomic group and a standardized field methodology across several cities around the world (Niemelä et al. 2002).

Specific measures also have an important role to play, as it is through an investigation of specific aspects of urbanization that we are able to begin identifying mechanisms or drivers of ecological responses, and thus can begin to identify concrete recommendations for managing and conserving ecological patterns and processes in urban areas. The combination of broad and specific measures that are used would be determined by the aims of the study being undertaken and the level of previous information available.

In light of the importance of broad measures of urbanization, it should be possible to identify a standard set of measures that could be used to quantify gradients for future studies. These common gradients could then be used to provide an 'urbanization context' to a particular study and would facilitate integration between studies. One of the key distinctions made in urban ecological literature is the difference between ecology 'in' cities and ecology 'of' cities (Grimm et al. 2000; Pickett et al. 2001). Ecology 'in' cities refers to small-scale, usually single-discipline studies within a city; and ecology 'of' cities incorporates socio-economic and human ecosystem elements to form an understanding of ecology at a broader, multi-disciplinary scale. Currently, most urbanization gradient studies would be considered to address the ecology 'in' cities. However, by providing a common measure of urbanization it may be possible to combine the outcomes of ecology 'in' cities studies to develop a better understanding of the ecology 'of' cities.

Our understanding of these broad measures of urbanization (e.g., density of people, land-use) is still developing. We still need a better understanding of which measures are being used most frequently, although the investigation by McIntyre et al. (2000) is a great starting point. We need to investigate how informative the different measures are for predicting the outcomes of particular studies, as well as their utility in integrating different studies. We also need to develop a better understanding of: (1) what are the most informative combinations of demographic measures, physical/chemical measures and quantitative landscape metrics; (2) how the characteristics (scale, typology) of the landscape classification system used will interact to influence the outcomes of the study; (3) the level of redundancy or correlation between selected measures and (4) the ability to attach a biological or ecological interpretation to the selected measure. Beginning to address these issues requires studies which examine the measures themselves. This would add a fertile new area of research for urbanization gradient studies.

The study of urbanization gradients

A search of the electronic bibliographic data bases that were available in May 2007 revealed some 300 papers that had explicitly utilised a gradient approach in studying the ecology of urbanizing landscapes. Independent of what the gradient was called, we included all papers that utilized an urbanization or anthropogenic gradient approach to address their research questions. Although researchers have used different terminology to refer to the gradients including land-use, urban-rural, wildland-urban, wildland-suburban and urban to exurban, they are all fundamentally referring to gradients of urbanization (Marzluff et al. 2001). The most commonly used measures of these landscape gradients were broad measures related to land-use or land-cover at both local and regional scales. There are certainly other published studies not captured in this search, but the objective of this section was to highlight some of the major topics of the studies. Here, we summarize the major findings related to the distribution and abundance of organisms along gradients of urbanization; however, this should not be considered a comprehensive review of the subject matter.

An examination of the compiled database of research conducted on gradients of urbanization revealed that most of the studies (63%) focused on the response of organisms to urbanization (Table 1). The other studies were grouped into five major categories which are listed here in descending order: pollution/disturbance/nutrient fluxes, spatial patterns, humans, general reviews and gradient quantification (Table 1). The pollution/disturbance/nutrient fluxes category includes primarily studies of soil, water and atmosphere. A significant number of these studies have been conducted along urbanization gradients in the eastern (Pouyat and McDonnell 1991; Carreiro et al. 1999; Lovett et al. 2000; Zhu and Carreiro 2004; Groffman et al. 2006) and western (Hope et al.

Table 1 Major topics of published research on gradients of urbanization

	Number of studies	% of studies
Distribution of organisms	201	63
Pollution/disturbance/nutrient flux	53	17
Spatial patterns	36	11
Humans (e.g., health, perceptions)	14	4
Reviews and research directions	10	3
Gradient quantification[a]	5	2
Total	319	

[a] Because there is a vast literature of GIS studies that quantify landscapes, we chose only to include those studies that specifically addressed issues related to urbanization gradients

2005; Jenerette et al. 2006; Allen et al. 2007) United States.

Spatial pattern studies focused on the abundance, pattern and distribution of landscape elements (e.g., green spaces, farmland, subdivisions, remnant patches, roads) present along the gradient (Kong and Nakagoshi 2006; De Clercq et al. 2007). The papers included in the human category addressed issues of human health (Howe et al. 1992) and the human dimensions of gradients of urbanization (Dow 2002). The reviews and directions category are characterized by the work of Niemelä (1999); Pickett and Cadenasso (2006) and Theobald (2004). Finally, the studies grouped in the gradient quantification category look at the measures themselves, how they changed with scale and whether they were useful to compare different cities (Luck et al. 2001; Cadenasso et al. 2007). The number of papers in this category is relatively small for we did not include the numerous papers that are about quantifying landscapes in general (Herzog and Lausch 2001; Wu 2004).

The organisms studied were very diverse and we cite only a few papers as examples due to space limitations. These studies include plants (Hope et al. 2003; Burton et al. 2005; Williams et al. 2005; Ziska and George 2007; Hahs and McDonnell 2007), birds (Blair 1996; Natuhara and Imai 1999; Marzluff and Ewing 2001; Chapman and Reich 2007), mammals (Bowers and Breland 1996; Odell and Knight 2001), insects (Blair and Launer 1997; Niemelä et al. 2002; Avondet et al. 2003; Piel et al. 2005; Sadler et al. 2006), micro-organisms (Pouyat et al. 1994; Vilisics et al. 2007), marine and freshwater invertebrates (Ourso and Frenzel 2003; Walsh 2006), terrestrial macro-invertebrates (Steinberg et al. 1997; Szlavecz et al. 2006; Holland et al. 2007), fungi (Pouyat et al. 1994; Cousins et al. 2003), fish (Limberg and Schmidt 1990; Fraker et al. 2002), reptiles (Germaine and Wakeling 2001; Koenig et al. 2001) and amphibians (Parris 2006) (Table 2).

Table 2 Types of organisms studied along gradients of urbanization

	Number of studies	% of studies
Birds	49	24
Insects	31	15
Plants	28	14
Multiple taxonomic groups	26	13
Species interactions	17	9
Mammals	13	7
Other terrestrial macroinvertebrates	12	6
Fish	9	5
Marine and freshwater invertebrates	9	5
Micro-organisms	5	3
Reptiles/amphibians	1	1
Fungi	1	1
Total	201	

Organism responses to urbanization gradients

In the early days of studying urban environments most ecologists would have hypothesized that organisms would, in general, exhibit a negative response to urbanization (McDonnell and Pickett 1993). From our review of the literature, the responses of organisms to urbanization gradients were not predictable and ranged the gamut of possibilities from negative to positive, and everything in between (Fig. 1). Hansen et al. (2005), in their study of the effects of exurban development on biodiversity in the US, reviewed the available literature and standardized the reported species responses to a wild-urban gradient. They found that in areas closer to the urban end of the gradient with increased housing densities, species richness of organisms such as arthropods, insects, and amphibians declined (i.e., negative response). Bird and butterfly species richness was highest at intermediate levels of urbanization. McKinney (2006) reviewed the urban–rural gradient literature and

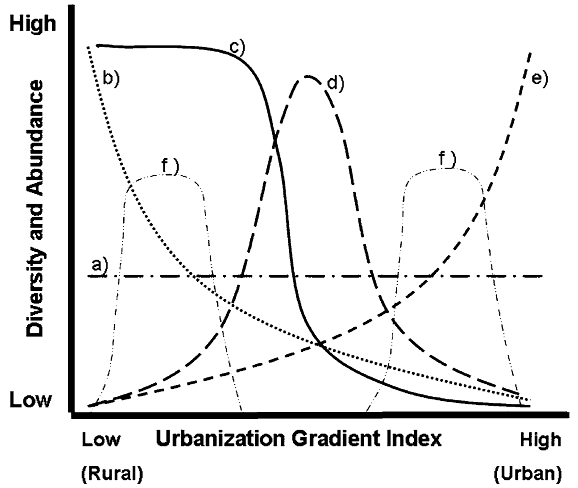

Fig. 1 Responses of organisms to gradients of urbanization. Key: (**a**) no response, (**b**) negative response, (**c**) punctuated response, (**d**) intermediate response, (**e**) positive response and (**f**) bimodal response

proposed that species richness, biotic interactions and ecosystem complexity decline toward the more urban end of the gradient whereas biomass, total organism abundance, biotic influences on abundance and ecosystem reliance on external subsidies increase with increasing urbanization.

In our database the most commonly studied taxa were birds, accounting for nearly 50% of all the organism studies (Table 2). Marzluff (2001), in a comprehensive review of published studies of the impact of urbanization on birds, found that, in general, bird species richness and evenness decreases, whereas density increases with increasing urbanization. The intermediate response of birds to gradients of urbanization has been reported by several researchers (Blair 1996; Allen and O'Connor 2000) and has been attributed to the diversity of habitats present in suburban environments. Blair (1996) refers to bird species that exhibit high abundance at intermediate levels of urbanization (i.e., suburban environments) as suburban adapters. McKinney (2002, 2006) categorizes urban biota as a function of their distribution and abundance along urbanization gradients: urban avoiders, urban adapters and urban exploiters. These categories of urban biota provide convenient labels for describing the pattern of biodiversity along gradients of urbanization, but the actual distribution of organisms along these gradients is context- and scale-dependent, and can be significantly affected by inter-specific competition. To develop better generalizations about the distributions of species along gradients of urbanisation it would be useful to adopt a standard set of broad urbanization measures that would provide a common context for the gradients, thereby standardizing the influence of the urbanization measure on the outcome of the studies.

The studies of bird species diversity and abundance along urbanization gradients have provided useful generalizations about the interactions between birds and human settlements and they serve as an excellent model for other organism studies to emulate. The existing bird studies have only scratched the surface of the level of understanding required to conserve and manage bird species diversity in an urbanizing world (Marzluff et al. 2001). Future studies need to address the fact that there are several mechanisms functioning at different scales affecting bird responses to urbanization, and it is important to define and elucidate the appropriate level of ecological functioning in order to enhance scientific understanding and conservation outcomes (Blair 2004; Marzluff 2005, Clergeau et al. 2006).

It was not the objective of this article, nor was there space, to summarize in detail all the species responses to urbanization gradients described in the studies in our database, but they were all assessed to compile a list of general trends (Fig. 1). The diversity of species responses indicates the existence of multi-causal factors and individualistic species responses (Gleason 1926) to urbanization gradients. The future identification of underlying causal factors and further explorations of species traits that influence the distribution of organisms along urbanization gradients will require integration of the gradient framework with the other ecological frameworks mentioned earlier (e.g., patch dynamics, the classic ecosystem approach, metapopulation dynamics, mechanistic studies and the human ecosystem model) (Faeth et al. 2005; Sadler et al. 2006). Additionally, it is important for researchers to move beyond pattern questions and address process questions (e.g., species performance (Williams et al. 2005) and trophic dynamics (Faeth et al. 2005).

Although there appear to be useful generalizations about the distribution of birds along urbanization gradients, there is a relative paucity of published studies on other organisms (Table 2). In fact, it was somewhat surprising not to discover more studies on mammals.

Insect studies on a global scale using the gradient approach, the same taxonomic group and field methodology have yielded understanding comparable to that of bird studies. The carabid beetles collected in woodlands in several cities showed some evidence of an increase in overall abundance and species richness from city centres to the rural surroundings, but no evidence of elevated diversity at suburban sites (Niemelä et al. 2002). When carabid species were classified into forest and open habitat species, a clear picture emerged; the proportion of forest habitat species decreased significantly from the surrounding rural environments to the city centres, while the proportion of open habitat species increased significantly towards the city centres. Furthermore, as predicted, the proportion of large sized carabid beetles decreased towards the city centres, so too did the proportion of short winged species (Niemelä et al. 2002).

Future research opportunities

In this final section, we will present examples of two additional studies that demonstrate how our understanding of urbanization gradients can be enhanced in the future.

Comparing urbanization gradients in different cities

One of the previously mentioned benefits of broad measures of urbanization is that they provide a common measure for comparing patterns of urbanization between cities or studies. For example, patterns of urbanization within Melbourne, Australia (Hahs and McDonnell 2006), can be compared with patterns of urbanization for Auckland, New Zealand, using a common broad measure of urbanization (Fig. 2). We chose to use a measure developed by Weeks et al. (2003) to represent the gradient based on our assessment of 17 commonly used measures of urbanization (Hahs and McDonnell 2006). The measure is based on combining two different indices relating to (1) the density of people working in non-agricultural industries obtained from census information (index census, Eqs. 1 and 2) the proportion of the landscape covered by impervious surfaces obtained from satellite imagery (index image, Eq. 2). Due to the formulae used to calculate these measures, their values fall between 0 and 100 regardless of the city or area being quantified. The final measure (index combined , Eq. 3) is the average of the two previous indices; where values between 0 and 15 represent sparse rural development, and values of 90–100

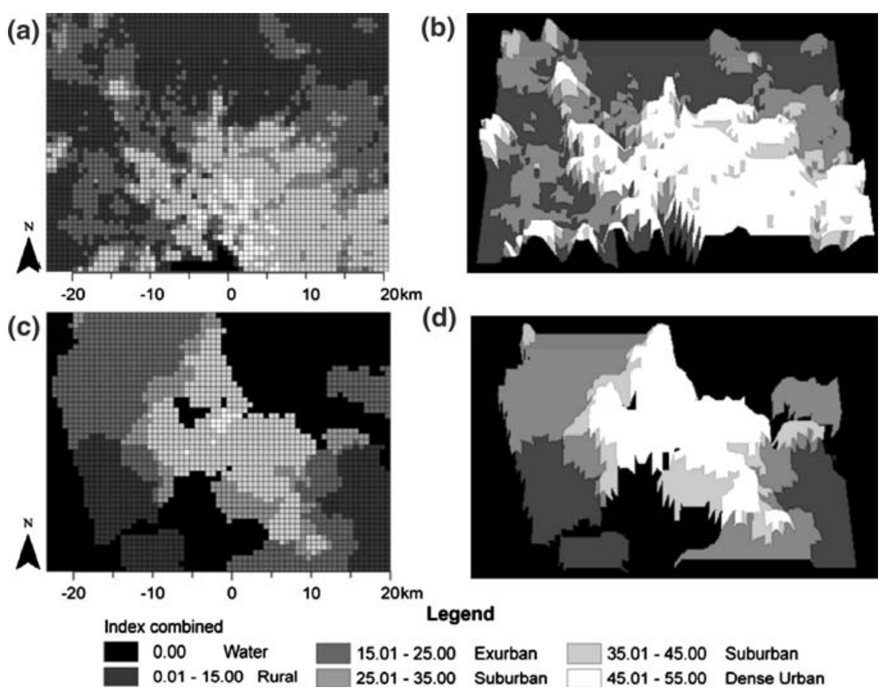

Fig. 2 Values of index combined across northern Melbourne, Australia, represented as (**a**) a two-dimensional grid, and (**b**) a three-dimensional representation of the same data, and the equivalent images for Auckland, New Zealand (**c**, **d**). In the 3D images (**b**, **d**) white represents index combined values of 35.01–55.00. Each pixel represents a 1 km × 1 km grid cell

represent highly urban environments, such as Cairo (e.g., 370,000 people per km^2; Weeks et al. 2003).

$$\text{Index}_{\text{census}} = \left\{ \frac{[\ln(D_{\text{p}}) \times P(\text{non}-\text{agr})]}{c} \right\} \times 100 \quad (1)$$

$$\text{Index}_{\text{image}} = C_i + \left(2 \times \sqrt{C_b}\right) + \left(2 \times \sqrt{C_s}\right) \quad (2)$$

$$\text{Index}_{\text{combined}} = \frac{(\text{Index}_{\text{census}} + \text{Index}_{\text{image}})}{2} \quad (3)$$

D_{p} is population density, P (non-agr) is number of males in non-agricultural jobs and c is constant (12.82); C_{i} is percent impermeable surface, C_{b} is percent bare ground and C_{s} is percent soil. See Hahs and McDonnell (2006) for a detailed explanation of the equations.

We used the combined measure as our previous analysis showed it explained more variability than either of the constituent measures alone. Interpreting the index combined values between 15 and 90 is more difficult as they can represent a combination of extensive built surfaces with few people (i.e., few males working in non-agricultural jobs), such as industrial areas, or high densities of people living in areas with a high amount of vegetation cover, such as high-rise apartments surrounded by large gardens. All of the indices we studied experience similar difficulties of interpretation (Hahs and McDonnell 2006). These indices (Eqs. 1, 2, and 3) are relatively easy to calculate and provide a dimensionless value that represents the intensity of urbanization which is very useful for the study of urbanization gradients within cities and between cities of different sizes.

For the purpose of this example, values of 45–55 represent highly urbanized environments with relatively high densities of people and built surfaces (urban), values of 25–45 represent moderate densities of people and built surfaces (suburban), and values of 15–25 represent relatively low densities of people and built surfaces (exurban). These labels for different values are not definitive. Melbourne and Auckland are relatively small, young cities on a global scale and most likely have lower index combined scores for their most intensely urban areas as opposed to much higher scores for older more densely populated, developed cities. Defining precise categories based on these measures is difficult as the measure is quite new and has not been widely applied by different research groups to different cities. We included the labels simply to provide a general description around the nature of the landscape each of the different values represent in Melbourne and Auckland.

When the value for index combined was calculated for 1 km^2 grid cells across both Melbourne and Auckland, it became apparent that both cities have a fairly concentrated distribution of higher values adjacent to their city centres. However, in Auckland, which is constrained by water on two sides, the highly urban landscapes show fewer urbanization valleys, compared to Melbourne, where the higher index combined values are intersected by lower values along the larger watercourses. Also, in Auckland, the higher index combined values are centred more tightly around the central business district (CBD), whereas in Melbourne, these higher values extend much further, particularly to the east of the CBD (Fig. 2).

The two cities can also be compared graphically as well as visually (Fig. 3). In Auckland, 35% of the study area is composed of water, whereas in Melbourne water covers only 1%. In Melbourne, 26% of the landscape is covered by areas with index combined values between 35 and 55, compared to Auckland, where these values cover only 17% of the landscape. Melbourne also has twice the area with index combined values of 0–15.

This example is still quite limited as it has only used one measure of urbanization to compare two cities with similar designs. Further research could be developed in this area by expanding the range of cities being investigated, particularly to include cities

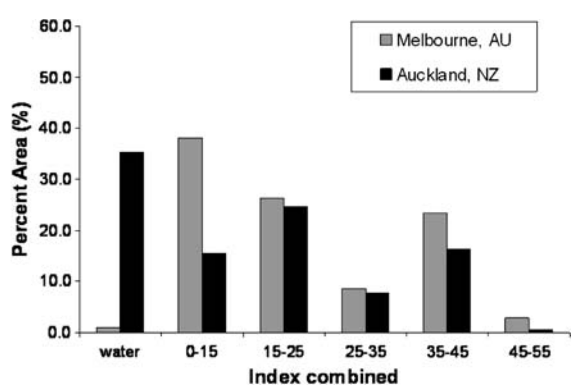

Fig. 3 Percent of the study area for Melbourne, Australia and Auckland, New Zealand, covered by water, and by five different categories of index combined values

in other parts of the world such as Europe, the Americas, Asia and Africa, where development patterns may differ to those of Australia and New Zealand. Also, the ability of different broad measures, such as those used by Hahs and McDonnell (2006) in Melbourne, to distinguish patterns between cities would provide valuable information on which measures may be most useful for including in a set of standard measures for future studies.

Investigating how different measures of urbanization influence tree species richness

Broad measures of urbanization are not restricted to defining an urban to rural gradient, they can also describe gradients within an urban area and can thus be used to investigate patterns within cities. When urbanization is represented as a continuous variable, the subtle variability across urban areas becomes apparent. It then becomes possible to examine how an ecological response varies across the 'mountains and valleys' within an urban area (Fig. 2). As an example, we investigated how the species richness of trees and shrubs >2 m in height varied across Melbourne with changing values of urbanization. As we had previously identified four independent measures of urbanization for Melbourne (Hahs and McDonnell 2006), we were also able to test which of these measures were the strongest predictors of species richness for this study.

The data we used were obtained from a field survey of native and introduced trees and shrubs within 400 m^2 quadrats in two different planning zones, which was undertaken over the period of August 2003 to June 2004. We focused on only two planning zones, residential and open space, to reduce the potential confounding site factors associated with the other planning zones. A total of 85 quadrats, 56 in the residential and 29 in the open space planning zones were established. Quadrats in the residential planning zone could be composed of buildings, roads, gardens or lawns. Quadrats in the open space planning zone could be located in sports fields, open parkland or remnant natural vegetation. For each quadrat, all plants >2 m in height were identified to species level (where possible) and their diameter at breast height was recorded. The values of the four independent measures of urbanization (index combined (IND), people per urban land cover (PeUr), landscape shape index (LSI) and dominant land cover) were calculated for a 1 km^2 circular area surrounding the centre point of each quadrat (see, Hahs and McDonnell 2006) for a detailed explanation of how the measures were calculated and what these measures represent). These data were then analyzed to assess their effect on species richness using Bayesian regression models (McCarthy 2007). The regression equation used for the full model was:

$$\log(\mathrm{SR}[i]) \sim a + a_{\mathrm{Zone}[i]} + a_{\mathrm{DOM}[i]} + b_{\mathrm{IND}} * \mathrm{IND}[i] + b_{\mathrm{PeUr}} * \mathrm{PeUr}[i] + b_{\mathrm{LSI}} * \mathrm{LSI}[i] \quad (4)$$

where SR[i] is the species richness at quadrat i, and the regression coefficients related to planning zone (a_{Zone}), dominant land cover (a_{DOM}), index combined (b_{IND}), people per urban land cover (b_{PeUr}) and LSI (b_{LSI}). Planning zone and dominant land cover were categorical variables and therefore treated differently in the equation than the other three continuous variables.

The full model and 16 additional models representing all possible combinations of the four urbanization measures, including a null model with no urbanization measures, were run for 100,000 iterations using uninformative priors. The performance of each model was evaluated using deviance information criterion (DIC) values (Spiegelhalter et al. 2002). The DIC values are a measure of fit between the model and the data. The model with the lowest DIC value has the greatest support, given the data.

To monitor the influence of each variable on the predictions, we calculated the effect size using the equation:

$$\text{Effect size}\,[i] = \exp(b[i] * \mathrm{range}[i]) \quad (5)$$

where $b[i]$ is the value of the regression coefficient, and range[i] is the range of values present for that variable within the data. As the predicted effect size deviates from 1, there is a larger magnitude of effect. For values >1 the effect is positive. For values <1 the effect is negative. An effect size of 1 indicates no effect. Due to the modelling equation we used, the two categorical variables were evaluated relative to a reference class, in this case, the residential zone was the reference class for planning zone, and impervious surface was the reference class for dominant land cover.

The best model for estimating the species richness of trees and shrubs was the full model excluding the LSI index variable. This indicates that there are fewer species of trees in the open space zone relative to the Residential zone (Fig. 4). The influence of dominant land cover varies depending on the nature of the land cover (Fig. 4). Plots in an area dominated by grassy land cover [DOM (grass)] had similar species richness to plots surrounded by areas dominated by impervious surface cover [DOM (built)], but plots in areas dominated by tree cover [DOM (tree)] had higher species richness relative to the other two landscape types. The effect of index combined was similar in magnitude to areas with trees as the dominant land cover [DOM (tree)] (Fig. 4). The influence of PeUr was negative, although the error bars indicate there could potentially be no effect of this variable (Fig. 4). As LSI was excluded from the best model, its effect size was set at 1, which represents no effect (Fig. 4). To summarize, tree and shrub diversity increases with increasing urbanization (e.g., higher combined Index score) but varies depending on dominant land cover type (Fig. 5). This study demonstrates that not only can urbanization gradients be used to investigate ecological patterns within cities, they can also be evaluated against additional variables, and their relative influence can be assessed.

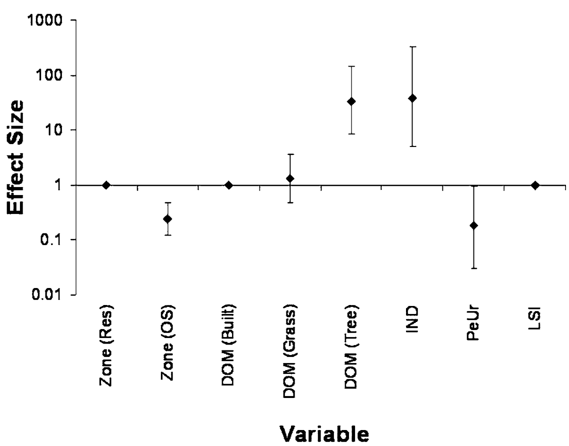

Fig. 4 The effect size of the different regression coefficients for the two planning zones (residential [Res] and open space [OS]); three dominant land cover (DOM) types (built, grass, tree); and the continuous variables of index combined (IND); people per unit urban land cover (PeUr) and landscape shape index (LSI). The effect sizes were used to examine how the species richness of trees and shrubs >2 m height varied with different measures of urbanization within Melbourne, Australia. Variables with an effect size of 1 show no effect. Effect sizes >1 indicate a positive effect, and <1 indicate a negative effect

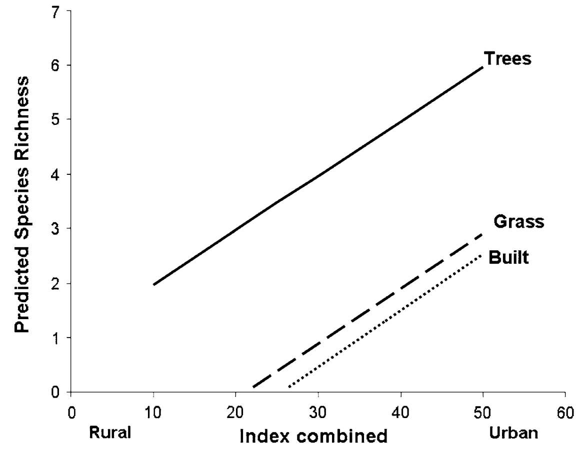

Fig. 5 Model predictions of the number of species of trees and shrubs in residential zoned areas of Melbourne as a function of Index combined scores and dominant land use type (i.e., tree, grass and built). People per urban land cover was held constant in the model

Summary

The study of urbanization gradients has made significant progress since the initial proposal by McDonnell and Pickett (1990). We now have a greater understanding of the response of many groups of organisms to urbanization, especially for birds, insects, plants and other terrestrial organisms. However, some taxonomic groups are severely understudied (e.g., fish, fungi, micro-organisms, reptiles, amphibians). While we can begin to develop generalizations about how organisms respond to urbanization gradients, these understandings will currently be biased towards larger, terrestrial organisms. The likelihood of generalities being equally applicable to smaller, more cryptic organisms is something that will need to be investigated in the future.

Similarly, our understanding of urbanization gradients can also benefit from new studies that investigate in greater detail the techniques used to quantify the gradient, and their implications for research findings. This paper has identified some of the issues involved in selecting broad measures of urbanization to represent the gradient, and has provided two examples of how these measures can begin to be investigated in greater detail. Future research efforts need to address the current knowledge gaps we have identified to ensure that future reviews of urbanization gradients do not suffer from similar taxonomic and research emphasis biases.

Acknowledgements The authors wish to thank Kelly Holland for her assistance in compiling the database on studies employing the urban-rural gradient approach. Rodney van der Ree, Ben Hamilton and Lauren Keim were instrumental in collecting the vegetation data. We would also like to thank Mick McCarthy and Kirsten Parris for their assistance with the Bayesian analysis. This manuscript was improved by comments from Zoë Smith, Julia Stammers, Briony Norton, Margaret Carreiro, Nancy McIntyre, Jari Niemelä and an anonymous reviewer. The Baker Foundation provided generous support for this research.

References

Alberti M (2008) Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. Springer, New York

Alberti M, Botsford E, Cohen A (2001) Quantifying the urban gradient: linking urban planning and ecology. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, MA, pp 89–115

Allen AP, O'Connor RJ (2000) Interactive effects of land use and other factors on regional bird distributions. J Biogeogr 27:889–900. doi:10.1046/j.1365-2699.2000.00453.x

Allen TFH, Wyleto EP (1983) A hierarchical model for the complexity of plant communities. J Theor Biol 101:529–540. doi:10.1016/0022-5193(83)90014-0

Allen EB, Temple PJ, Bytnerowicz A, Arbaugh MJ, Sirulnik AG, Rao LE (2007) Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution. Sci World J 7:247–263. doi:10.1100/tsw.2007.72

Avondet JL, Blair RB, Berg DJ, Ebbert MA (2003) *Drosophila* (Diptera: Drosophilidae) response to changes in ecological parameters across an urban gradient. Environ Entomol 32:347–358

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl 6:506–519. doi:10.2307/2269387

Blair RB (2004) The effects of urban sprawl on birds at multiple levels of biological organization. Ecol Soc 9:2

Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. Biol Conserv 80:113–125. doi:10.1016/S0006-3207(96)00056-0

Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. Ecol Appl 6:1135–1142. doi:10.2307/2269597

Burton ML, Samuelson LJ, Pan S (2005) Riparian woody plant diversity and forest structure along an urban–rural gradient. Urban Ecosyst 8:93–106. doi:10.1007/s11252-005-1421-6

Cadenasso ML, Pickett STA, Schwarz K (2007) Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. Front Ecol Environ 5:80–88. doi:10.1890/1540-9295(2007)5[80:SHIUER]2.0.CO;2

Carreiro MM, Howe K, Parkhurst DF, Pouyat RV (1999) Variation in quality and decomposability of red oak leaf litter along an urban–rural gradient. Biol Fertil Soils 30:258–268. doi:10.1007/s003740050617

Chapman KA, Reich PB (2007) Land use and habitat gradients determine bird community diversity and abundance in suburban, rural and reserve landscapes of Minnesota, USA. Biol Conserv 135:527. doi:10.1016/j.biocon.2006.10.050

Clergeau P, Jokimäki J, Snep R (2006) Using hierarchical levels for urban ecology. Trends Ecol Evol 21:660–661. doi:10.1016/j.tree.2006.09.006

Collins JP, Kinzig A, Grimm NB, Fagan WF, Hope D, Wu J et al (2000) A new urban ecology. Am Sci 88:416–425. doi:10.1511/2000.5.416

Cousins JR, Hope D, Gries C, Stutz JC (2003) Preliminary assessment of arbuscular mycorrhizal fungal diversity and community structure in an urban ecosystem. Mycorrhiza 13:319–326. doi:10.1007/s00572-003-0239-4

De Clercq EM, De Wulf R, Van Herzele A (2007) Relating spatial pattern of forest cover to accessibility. Landsc Urban Plan 80:14–22. doi:10.1016/j.landurbplan.2006.04.007

Dow K (2002) Social dimensions of gradients in urban ecosystems. Urban Ecosyst 4:255–275. doi:10.1023/A:1015767231137

Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. Bioscience 55:399–407. doi:10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

Fraker ME, Snodgrass JW, Morgan F (2002) Differences in growth and maturation of blacknose dace (*Rhinichthys atratulus*) across an urban–rural gradient. Copeia 2002:1122–1127. doi:10.1643/0045-8511(2002)002[1122:DIGAMO]2.0.CO;2

Germaine SS, Wakeling BF (2001) Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol Conserv 97:229–237. doi:10.1016/S0006-3207(00)00115-4

Gilbert OL (1989) The ecology of urban habitats. Chapman and Hall, London

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7–26. doi:10.2307/2479933

Grimm NB, Grove JM, Pickett STA, Redman CA (2000) Integrated approaches to long-term studies of urban ecological systems. Bioscience 50:571–584. doi:10.1641/0006-3568(2000)050[0571:IATLTO]2.0.CO;2

Groffman PM, Pouyat RV, Cadenasso ML, Zipperer WC, Szlavecz K, Yesilonis ID et al (2006) Land use context and natural soil controls on plant community composition and soil nitrogen and carbon dynamics in urban and rural forests. For Ecol Manage 236:177–192. doi:10.1016/j.foreco.2006.09.002

Hahs AK, McDonnell MJ (2006) Selecting independent measures to quantify Melbourne's urban–rural gradient. Landsc Urban Plan 78:435–448. doi:10.1016/j.landurbplan.2005.12.005

Hahs AK, McDonnell MJ (2007) Composition of the plant community in remnant patches of grassy woodland along

an urban-rural gradient in Melbourne, Australia. Urban Ecosyst 10:355–377. doi:10.1007/s11252-007-0034-7
Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH et al (2005) Effects of exurban development on biodiversity: patterns mechanisms, and research needs. Ecol Appl 15:1893–1905. doi:10.1890/05-5221
Herzog F, Lausch A (2001) Supplementing land-use statistics with landscape metrics: some methodological considerations. Environ Monit Assess 72:37–50. doi:10.1023/A:1011949704308
Holland KD, McDonnell MJ, Williams NSG (2007) The potential impact of mollusk herbivory on native grasslands in Victoria, Australia. Aust Ecol 32:626–634
Hope D, Gries C, Zhu WX, Fagan WF, Redman CL, Grimm NB et al (2003) Socioeconomics drive urban plant diversity. Proc Natl Acad Sci USA 100:8788–8792. doi:10.1073/pnas.1537557100
Hope D, Zhu W, Gries C, Oleson J, Kaye J, Grimm N et al (2005) Spatial variation in soil inorganic nitrogen across an arid urban ecosystem. Urban Ecosyst 8:251–273. doi:10.1007/s11252-005-3261-9
Howe HL, Katterhagen JG, Yates J, Lehnherr M (1992) Urban–rural differences in the management of breast cancer. Cancer Causes Control 3:533–539. doi:10.1007/BF00052750
Jenerette GD, Wu JG, Grimm NB, Hope D (2006) Points, patches, and regions: scaling soil biogeochemical patterns in an urbanized arid ecosystem. Glob Change Biol 12:1532–1544. doi:10.1111/j.1365-2486.2006.01182.x
Jerzak L (2001) Synurbanization of the magpie in the Palearctic. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, Massachusetts, pp 403–425
Kinzig AP, Grove JM (2001) Urban-suburban ecology. In: Levin SA (ed) Encyclopedia of biodiversity. Academic Press, San Diego, pp 733–745
Koenig J, Shine R, Shea G (2001) The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? Wildl Res 28:215–227. doi:10.1071/WR00068
Kong F, Nakagoshi N (2006) Spatial–temporal gradient analysis of urban green spaces in Jinan, China. Landsc Urban Plan 78:147–164. doi:10.1016/j.landurbplan.2005.07.006
Limberg KE, Schmidt RE (1990) Patterns of fish spawning in Hudson River tributaries: response to an urban gradient? Ecology 71:1238–1245. doi:10.2307/1938260
Lovett GM, Traynor MM, Pouyat RV, Carreiro MM, Zhu WX, Baxter JW (2000) Atmospheric deposition to oak forests along an urban–rural gradient. Environ Sci Technol 34:4294–4300. doi:10.1021/es001077q
Luck M, Wu J (2002) A gradient analysis of urban landscape pattern: a case study from the Phoenix metropolitan region, Arizona, USA. Landsc Ecol 17:327–339. doi:10.1023/A:1020512723753
Luck MA, Jenerette GD, Wu JG, Grimm NB (2001) The urban funnel model and the spatially heterogeneous ecological footprint. Ecosystems 4:782–796. doi:10.1007/s10021-001-0046-8 (NY, Print)
Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, Massachusetts, pp 19–47
Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human dominated landscapes. Urban Ecosyst 8:157–177. doi:10.1007/s11252-005-4378-6
Marzluff JM, Ewing K (2001) Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restor Ecol 9:280–292. doi:10.1046/j.1526-100x.2001.009003280.x
Marzluff JM, Bowman R, Donnelly R (2001) A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, Massachusetts, pp 1–17
McCarthy MA (2007) Bayesian methods for ecologists. Cambridge University Press, Cambridge
McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. Ecology 71:1232–1237. doi:10.2307/1938259
McDonnell MJ, Pickett STA, Pouyat RV (1993) The application of the ecological gradient paradigm to the study of urban effects. In: McDonnell MJ, Pickett STA (eds) Humans as components of ecosystems. Springer-Verlag, New York, pp 175–189
McDonnell MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV, Zipperer WC et al (1997) Ecosystem processes along an urban-to-rural gradient. Urban Ecosyst 1:21–36. doi:10.1023/A:1014359024275
McIntyre NE, Knowles-Yanez K, Hope D (2000) Urban ecology as an interdisciplinary field: differences in the use of "urban" between the social and natural sciences. Urban Ecosyst 4:5–24. doi:10.1023/A:1009540018553
McKinney ML (2002) Urbanization, biodiversity and conservation. Bioscience 52:883–890. doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2
McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. doi:10.1016/j.biocon.2005.09.005
Natuhara Y, Imai C (1999) Prediction of species richness of breeding birds by landscape-level factors of urban woods in Osaka Prefecture, Japan. Biodivers Conserv 8:239–253. doi:10.1023/A:1008869410668
Niemelä J (1999) Is there a need for a theory of urban ecology? Urban Ecosyst 3:57–65. doi:10.1023/A:1009595932440
Niemelä J, Kotze DJ, Venn S, Penev L, Stoyanov I, Spence J et al (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: an international comparison. Landsc Ecol 17:387–401. doi:10.1023/A:1021270121630
Odell EA, Knight RL (2001) Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conserv Biol 15:1143–1150. doi:10.1046/j.1523-1739.2001.0150041143.x
Ourso RT, Frenzel SA (2003) Identification of linear and threshold responses in streams along a gradient of

urbanization in Anchorage, Alaska. Hydrobiologia 501:117–131. doi:10.1023/A:1026211808745

Parris KM (2006) Urban amphibian assemblages as metacommunities. J Anim Ecol 75:757–764. doi:10.1111/j.1365-2656.2006.01096.x

Pickett STA, Cadenasso ML (2006) Advancing urban ecological studies: frameworks, concepts, and results from the Baltimore ecosystem study. Aust Ecol 31:114–125. doi:10.1111/j.1442-9993.2006.01586.x

Pickett STA, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC et al (2001) Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annu Rev Ecol Syst 32:127–157. doi:10.1146/annurev.ecolsys.32.081501.114012

Piel F, Gilbert M, Franklin A, Gregoire JC (2005) Occurrence of *Ips typographus* (Col., Scolytidae) along an urbanization gradient in Brussels, Belgium. Agric For Entomol 7:161–167

Pouyat RV, McDonnell MJ (1991) Heavy-metal accumulations in forest soils along an urban-rural gradient in southeastern New York, USA. Water Air Soil Pollut 57–58:797–807. doi:10.1007/BF00282943

Pouyat RV, Parmelee RW, Carreiro MM (1994) Environmental effects of forest soil-invertebrate and fungal densities in oak stands along an urban-rural land-use gradient. Pedobiologia (Jena) 38:385–399

Sadler JP, Small EC, Fiszpan H, Telfer MG, Niemelä J (2006) Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. J Biogeogr 33:1126–1138. doi:10.1111/j.1365-2699.2006.01476.x

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191. doi:10.1016/j.tree.2005.11.019

Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. J R Stat Soc B 64:583–639. doi:10.1111/1467-9868.00353

Steinberg DA, Pouyat RV, Parmelee RW, Groffman PM (1997) Earthworm abundance and nitrogen mineralization rates along an urban–rural land use gradient. Soil Biol Biochem 29:427–430. doi:10.1016/S0038-0717(96)00043-0

Sukopp H (1998) Urban ecology: scientific and practical aspects. In: Breuste J, Feldmann H, Uhlmann O (eds) Urban ecology. Springer-Verlag, Berlin, pp 3–16

Szlavecz K, Placella SA, Pouyat RV, Groffman PM, Csuzdi C, Yesilonis I (2006) Invasive earthworm species and nitrogen cycling in remnant forest patches. Appl Soil Ecol 32:54–62. doi:10.1016/j.apsoil.2005.01.006

ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–317. doi:10.1016/S0065-2504(08)60183-X

Theobald DM (2004) Placing exurban land-use change in a human modification framework. Front Ecol Environ 2:139–144

Vilisics F, Elek Z, Lövei GL, Hornung E (2007) Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark. Pedobiologia (Jena) 51:45–53. doi:10.1016/j.pedobi.2006.12.004

Walsh CJ (2006) Biological indicators of stream health using macroinvertebrate assemblage composition: a comparison of sensitivity to an urban gradient. Mar Freshw Res 57:37–47. doi:10.1071/MF05041

Weeks JR, Larson D, Rashed T (2003) Contrast or continuum? The creation and application of an urban gradient index using remotely sensed imagery and GIS. Paper presented at the annual meeting of the population association of America, Minneapolis, pp 1–44

Whittaker RH (1967) Gradient analysis of vegetation. Biol Rev Cambr Philos Soc 49:207–264. doi:10.1111/j.1469-185X.1967.tb01419.x

Williams NSG, Morgan JW, McDonnell MJ, McCarthy MA (2005) Plant traits and local extinctions in natural grasslands along an urban-rural gradient. J Ecol 93:1203–1213. doi:10.1111/j.1365-2745.2005.01039.x

Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. Landsc Ecol 19:125–138. doi:10.1023/B:LAND.0000021711.40074.ae

Zhu WX, Carreiro MA (2004) Temporal and spatial variations in nitrogen transformations in deciduous forest ecosystems along an urban–rural gradient. Soil Biol Biochem 36:267–278. doi:10.1016/j.soilbio.2003.09.013

Zipperer WC, Wu JG, Pouyat RV, Pickett STA (2000) The application of ecological principles to urban and urbanizing landscapes. Ecol Appl 10:685–688. doi:10.1890/1051-0761(2000)010[0685:TAOEPT]2.0.CO;2

Ziska LH, George K (2007) Establishment and persistence of common ragweed (*Ambrosia artemisiifolia* L.) in disturbed soil as a function of an urban–rural macroenvironment. Glob Change Biol 13:266–274. doi:10.1111/j.1365-2486.2006.01264.x