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The Distinguishing Features of the Study of the Ecology of Urban Landscapes

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Abstract
The urban transformation of the planet has spurred interest across a wide variety of disciplines in the fundamental changes to human society and the environment that result from urbanization. Landscape ecology is no exception. Since the late 1980s, the number of papers devoted to the study of the ecology of urban landscapes has risen dramatically. This trend prompted the question I address in this paper: what are the distinguishing features of the study of the ecology of urban landscapes? To answer this question, I reviewed 894 papers, published between 1987 and 2011, describing the ecology of urban terrestrial landscapes. Landscape ecologists who study urban landscapes use the gradient paradigm and the urban ecosystem framework to shape their research questions. They study subjects such as land use/land cover change, the ecological effects of land use type and pattern, and human-made habitats that receive less attention from landscape ecologists studying non-urban areas. They also study a very wide variety of disturbances that occur in urban landscapes. And, increasingly, they are making use of citizen-generated data to answer their questions. Knowledge of the ecology of urban landscapes is largely based on comparisons of land use types, investigations along the urban gradient, and research centered on remnant habitat fragments in an urban matrix. Future directions for the study of the ecology of urban landscapes include testing whether understanding derived in less modified landscapes can be applied to intensively modified urban landscapes, investigating the interactions between agents of global change, such as climate change, and urbanization, investigating the effects of matrix quality on the biodiversity of habitat fragments, expanding our understanding of the ecological effects of land use pattern, and assessing the trade-offs between human needs and the needs of other species by means of transdisciplinary collaborations.

Introduction

The last two centuries have witnessed the transformation of the global human population from a rural to urban one. More than half of the global human population now resides in urban areas (United Nations 2009). This statistic dissimulates the spatial and temporal variation in the urban transformation of the planet. By 1950, the more developed regions of the world had populations that were already more than half urban (Figure 1a). At that time, urban dwellers in the more developed parts of the world represented approximately 60% of the global urban population. Since 1950, the greatest growth in urban populations has been in the less developed parts of the world (Figure 1b). Consequently, the number of urban dwellers in the less developed parts of the world now makes up approximately three-quarters of the total number of urban dwellers on the planet.

The urban transformation of the planet has spurred interest across a wide variety of disciplines in the fundamental changes to human society and the environment that result from urbanization. Social scientists investigate the informal political and economic structures that have emerged in the vast slum neighborhoods in which one third of global urban inhabitants reside (Chatterjee 2010). Climatologists study the warmer atmospheric conditions

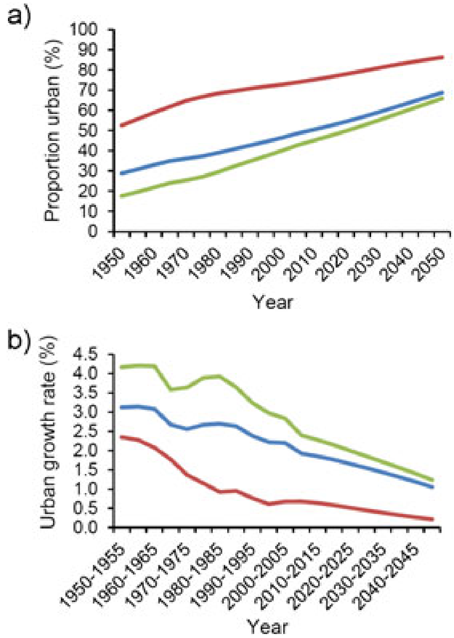

Fig 1. The percentage of the total human population residing in urban areas (a) and the average annual rate of change of the urban population (b) over time for the world (blue lines), more developed regions (red lines), and less developed regions (green lines). Data from United Nations (2009).

that characterize cities compared to the countryside (Arnfield 2003). Evolutionary biologists describe the adaptation of plant and bird species to new selection pressures in urban areas (Partecke and Gwinner 2007; Rios et al. 2008).

Landscape ecology has also embraced the study of urban areas. I carried out a Web of Science literature search in October of 2011 and identified 894 papers published between 1987 and 2011 describing the ecology of urban terrestrial landscapes (out of 3573 papers that included the keywords urban* and landscape*; see below for identification criteria). The number of papers published per year rose from one in the late 1980s to over 90 by the late 2000s (Figure 2). Two major influences have lead to the growing focus in landscape ecology on urban areas. First, the emergence of landscape ecology as a sub-discipline in the 1970s and 1980s coincided in large part with a broader paradigm shift in ecology as a whole. Ecology has transitioned from the study of pristine ecosystems in equilibrium with the environment to the study of dynamic systems that include humans and their activities as components (Wu and Loucks 1995). The establishment of the Central Arizona Phoenix Long-Term Ecological Research project and the Baltimore Ecosystem Study is evidence of this shift in thinking (Grimm et al. 2000). Second, landscape ecology has strong roots in the European geography and land use planning traditions (e.g., Troll 1950), which necessarily take into account the long history of human settlement in the region. These beginnings resulted in landscape ecology being characteristically focused on the structure and ecology of human-dominated landscapes and, more recently, on urban areas in particular.

The ever-increasing focus in landscape ecology on urban areas has prompted the question I address in this paper: what are the distinguishing features of the study of the ecology of urban landscapes? I begin by investigating the motivations behind studying the ecology of urban landscapes and describing the structure of urban landscapes. I then highlight the

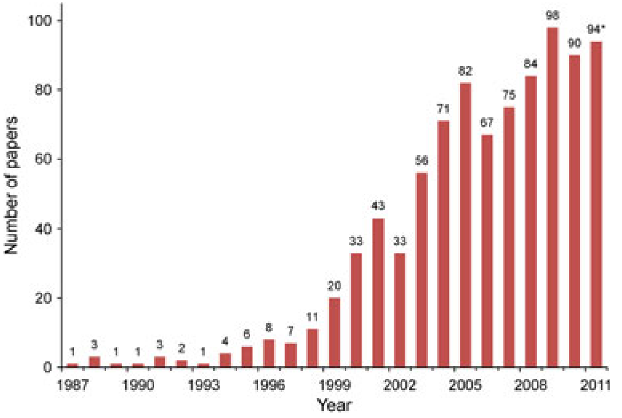

Fig 2. The number of papers describing the ecology of urban terrestrial landscapes published per year according to a Web of Science literature search carried out in October of 2011. *The datum for 2011 is representative of only a portion of that year.

features, such as paradigms, subjects of study, and approaches, that distinguish the study of the ecology of urban landscapes from landscape ecological research carried out in non-urban areas. Finally, I summarize the current understanding of the ecology of urban landscapes and suggest future research directions for the field.

To answer the question I address in this paper, I identified research on the ecology of urban landscapes, that is, the 894 papers resulting from the literature search mentioned above, as that conforming to particular definitions of landscape ecology, landscape, and urban area. I used the definition of landscape ecology suggested by Fahrig (2005): "the study of how landscape structure affects (the processes that determine) the abundance and distribution of organisms." Abiotic (e.g., wind) and biotic (e.g., primary production) processes are included in this definition and interactions among landscape structure, processes, and organismal patterns are reciprocal. In selecting papers, I modified the definition slightly to include the interactions between landscape structure and abiotic patterns (e.g., temperature patterns associated with the urban heat island effect). I also chose to include papers that simply quantified landscape structure or described land use/land cover change over time and did not investigate the interactions among landscape structure and abiotic and biotic patterns and processes. My use of Fahrig's (2005) definition of landscape ecology resulted in the selection of research focused mainly on organismal patterns and processes over space. Thus, in the present work, I do not consider topics such as landscape planning and landscape architecture that are considered by many to be included in a holistic definition of landscape ecology (e.g., Wu 2008). I used broad definitions of landscape and urban area. Turner et al. (2001) defined the former as an "area that is spatially heterogeneous in at least one factor of interest." For the latter, I considered a study area urban if it matched any of the areas comprising an urban ecosystem as defined by Pickett et al. (2001), namely "suburban areas, exurbs, sparsely settled villages connected by commuting corridors or by utilities, and hinterlands directly managed or affected by the energy and material from the urban core and suburban lands", or if it conformed to the definition of urban areas proposed by Gaston (2010) as including "towns, cities, and associated infrastructure." I limited my selection of papers to work carried out in terrestrial environments and did not consider research on road effects. Although urbanization and roads go hand in hand, roads are also located in non-urbanized regions and their effects are best summarized separately from those of urbanization. Finally, some relevant papers that I was previously aware of were not included in the 3573 papers resulting from the Web of Science literature search. I have taken the liberty of referring to these, as well as literature cited by the 894 papers I identified, in the following discussion.

Why Study the Ecology of Urban Landscapes?

Three major reasons likely motivate landscape ecologists to carry out research in urban areas. First, landscape ecologists may be drawn to urban areas because research in urban areas may facilitate transdisciplinarity, which is necessary for solving complex problems and achieving sustainability (Wu 2008). The interactions between people and nature in urban areas are often complex. The application of a landscape ecological approach, which easily integrates theories and methods from a variety of fields, to the investigation of these interactions offers the promise of transdisciplinarity and enhanced problem-solving capacity. Second, increased knowledge and understanding of the ecology of urban landscapes has the potential to significantly influence the conservation of biological diversity worldwide. Landscape ecologists studying urban areas can play a role in increasing the awareness and understanding of the ecology of urban landscapes among the general public. Since urban areas are increasingly the realms in which the majority of humanity lives, this increased awareness and understanding can translate into environmental awareness and action on a global scale (Dunn et al. 2006). Third, urban landscapes are among the most heterogeneous landscapes on the planet (see below). As inquirers into the interactions between spatial heterogeneity and ecological patterns and processes, landscape ecologists are likely drawn to urban areas for this reason.

The Structure of Urban Landscapes

Forman and Godron (1986) described changes in landscape structure along a gradient of human modification. Five landscape types that represented increasing human impacts characterized the gradient: natural, managed, cultivated, suburban, and urban. Forman and Godron (1986) predicted that average patch size and patch size variance would decrease along the gradient, the latter more rapidly than the former, and that regularity in patch shape and patch density would increase along the gradient. They concluded that human influences generally increase landscape heterogeneity, except where these are particularly heavy. Of the five landscape types considered, suburban landscapes, with their mix of natural and managed ecosystems, croplands, and residential and commercial areas, were predicted to be the most heterogeneous.

Ninety-four of the papers that I identified (11%) were focused solely on the quantification of landscape structure in urban areas, that is, they did not investigate the interactions among landscape structure and abiotic and biotic patterns and processes (Table 1). A subset of these quantified changes in landscape structure along urban gradients using landscape-level metrics (Table 2). The urban gradient, extending from the rural areas or wildlands surrounding a city to its core, has been a very popular subject of study since its introduction by McDonnell and Pickett (1990) and will be discussed in more detail in the next section. The results of the studies that quantified landscape structure along urban gradients indicate that landscape heterogeneity tends to increase with increasing urbanization (Table 2). Although changes in area metrics along the urban gradient indicate decreasing heterogeneity with increasing urbanization (Andersson et al. 2009; Antrop and Van Eetvelde 2000), changes in patch number and density, mean patch size, and patch size variability generally conform to the predictions of Forman and Godron (1986), indicating a positive association between landscape heterogeneity and urbanization (Andersson et al. 2009; Cifaldi et al. 2004; du Toit and Cilliers 2011; Luck and Wu 2002; Weng 2007; Wu et al. 2006). In addition, there is some evidence that edge density increases with increasing urbanization (Cifaldi et al. 2004).

Table 1. Topics addressed in the 894 papers describing the study of the ecology of urban terrestrial landscapes (see the text for paper identification criteria).

Topic	Number of papers	Percent of papers
Topics that distinguish the study of the ecology of urban landscapes from the study of the ecology of non-urban landscapes		
Land use/land cover change over time	240	26.8
Urban gradient	199	22.3
Ecological effects of land use type	69	7.7
Disturbance	63	7.0
Human-made habitats	25	2.8
Urban ecosystem	14	1.6
Citizen science	5	0.6
Ecological effects of land use pattern	4	0.4
Other topics		
Quantification of landscape structure	94	10.5
Habitat fragmentation	66	7.4
Non-native species	49	5.5
Species demography	35	3.9
Habitat selection	30	3.4
Species interactions	28	3.1
Species movement	26	2.9
Ecosystem functioning	24	2.7
Edge effects	20	2.2
Urban forest	18	2.0
Community homogenization	17	1.9
Island biogeography	14	1.6
Landscape genetics	14	1.6
Connectivity	12	1.3
Ecosystem services	10	1.1
Land use legacies	10	1.1
Metapopulation biology	9	1.0
Conservation corridors	8	0.9
Conservation biology	7	0.8
Species traits	5	0.6
Landscape epidemiology	4	0.4
Relative importance of landscape and local factors	4	0.4
Species distribution modeling	3	0.3
Biodiversity congruence	2	0.2
Climate change	2	0.2
Landscape modeling	2	0.2
Spatial scale	2	0.2
Species behavior	1	0.1
Body size	1	0.1
Sustainable development	1	0.1

A single paper may have addressed several topics. Topics are split into those that distinguish the study of the ecology of urban landscapes from the study of the ecology of non-urban landscapes and other topics that are equally likely to be addressed in urban as in non-urban landscapes.

Contrary to Forman and Godron's (1986) predictions, shape complexity generally increases with increasing urbanization (Andersson et al. 2009; Antrop and Van Eetvelde 2000; Luck and Wu 2002). Changes in diversity metrics along the urban gradient provide roughly equal support for increasing (du Toit and Cilliers 2011; Luck and Wu 2002; Weng 2007;

Wu et al. 2006) or decreasing (Andersson et al. 2009; Antrop and Van Eetvelde 2000; Wang et al. 2009) heterogeneity with increasing urbanization. Finally, the fragmentation ratio, which represents the degree to which the landscape is subdivided by linear patches, increased with increasing urbanization (Young and Jarvis 2001).

As suggested by Forman and Godron (1986), landscape heterogeneity may peak at intermediate levels of urbanization, that is, in suburban or peri-urban landscapes on the fringes of cities (Antrop and Van Eetvelde, 2000; Cifaldi et al. 2004; du Toit and Cilliers 2011; Wu et al. 2006; Table 2, Figure 3). This pattern is exemplified by the results of a study

Table 2. The responses of landscape-level metrics to increasing urbanization along urban gradients.

Landscape metric	Response to increasing urbanization
Area metrics	
Patch area	↑[1]
Largest patch index	↑[2], ↓[3]
Patch density, patch size, and variability metrics	
Number of patches	↑[2,3]
Patch density	↑[4,5,6], ∩[7]
Mean patch size	↓[4,5,7]
Patch size standard deviation	↓[7]
Patch size coefficient of variation	↑[5], ↓[6]
Edge metric	
Edge density	↑[6], ∩[7]
Shape metrics	
Landscape shape index	↑[2,5], ↓[8], ∩[3,7]
Area-weighted mean shape index	↑[5], ∩[7]
Corrected perimeter–area shape index (equal to $0.282*P/A^{0.5}$ where P is the perimeter and A is the area of a patch)	↑[1]
Fractal dimension [equal to the slope of the regression of log (patch perimeter) on log (patch area)]	↓[1]
Area-weighted mean patch fractal dimension	∩[7]
Diversity metrics	
Shannon's diversity index (of path types)	↑[7], ↓[1,9]
Shannon's diversity index (of land covers)	∩[1]
Simpson's diversity index	↑[3], ↓[2]
Patch richness	↑[3,5]
Shannon's evenness index	↑[4], ∩[7]
Landscape evenness index (ratio of actual value of Shannon's diversity index of patch types to its maximum value achieved when each patch type occupies the same proportion of the landscape)	↓[9]
Dominance (1 − Shannon's evenness index)	∪[6]
Landscape dominance index (difference between the maximum value of Shannon's diversity index of patch types achieved when each patch type occupies the same proportion of the landscape and its actual value)	↑[9]

(Continues)

Table 2. (Continued)

Landscape metric	Response to increasing urbanization
Contagion and interspersion metrics	
Interspersion and juxtaposition index	∩[6]
Contagion index	∪[7]
Fragmentation metric	
Fragmentation ratio (the quotient of the number of edges between linear patches and non-linear patches and the number of edges between non-linear patches; represents the degree to which the landscape is subdivided by linear patches)	↑[10]

Metrics were calculated using the formulas of McGarigal and Marks (1995) and follow their terminology except where otherwise noted.
[1]Antrop and Van Eetvelde (2000).
[2]Andersson et al. (2009).
[3]du Toit and Cilliers (2011).
[4]Weng (2007).
[5]Luck and Wu (2002).
[6]Cifaldi et al. (2004).
[7]Wu et al. (2006).
[8]Hahs and McDonnell (2006).
[9]Wang et al. (2009).
[10]Young and Jarvis (2001).

of landscape structural change along urban gradients in Beijing, China (Wu et al. 2006). Beijing's center is occupied by a once-fortified inner city, constructed during the Ming Dynasty (1368–1644 CE). The inner city has a rectangular land use pattern dominated by residential, institutional, commercial, and service-oriented land uses. Since 1949 and the establishment of the People's Republic of China, Beijing has expanded outward from the older inner city. Wu et al. (2006) reported that spatial heterogeneity, as measured by patch density, edge density, landscape shape index, area-weighted mean shape index, area-weighted mean patch fractal dimension, Shannon's evenness index, and the contagion index, increased from

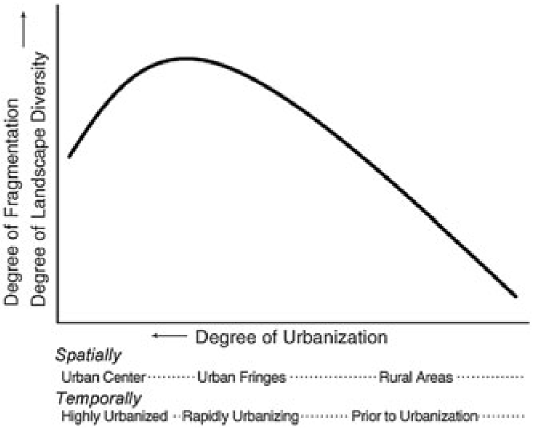

Fig 3. The hypothesized relationship between landscape heterogeneity, represented by fragmentation and landscape diversity, and degree of urbanization. Spatial and temporal patterns of urbanization influence landscape heterogeneity. Reproduced from Weng (2007) with permission.

the rural areas surrounding Beijing to the edge of the inner city and then declined within the inner city (Table 2). Thus, it appears that spatial heterogeneity may be maximal in the rapidly developing middle and outer areas of a city, where the variety of land covers and uses is greatest, such as in Forman and Godron's (1986) suburban landscapes. As urbanization proceeds through time and space, city centers, such as Beijing's inner city, become progressively dominated by built structures and one or a few land uses, resulting in more homogeneous landscape structure (Figure 3). The work of Thomas et al. (2008) provides evidence to this effect. The authors measured the fractal dimension (*D*; in this case, a measure of uniformity of pattern and not shape complexity as in Table 2) of patterns of built structures near Brussels, Belgium. With increasing urbanization (densification of built structures), *D* of surfaces increased and *D* of borders declined, indicating an increasingly homogeneous pattern of urban development.

The generality of the patterns described above may be limited by aspects of study design that have been suggested to inhibit the comparison of landscape structure among cities: the grain size and extent of the analysis, the classification typology, the accuracy of input data, the equations used to calculate measures of landscape structure, the type of statistical analysis, and the habitat context (du Toit and Cilliers 2011). For example, Weng (2007) found different patterns of landscape structural change along the halves of an urban gradient centered on the city of Madison, USA, and terminating in differing contexts. The west end of the gradient encompassed what is known as the Driftless Area, a hilly forested region unaffected by glacial activity, whereas the east end of the gradient was dominated by agriculture. Landscape structural change from the east end of the gradient towards the center of Madison conforms to the general pattern of increasing heterogeneity with increasing urbanization (Table 2). Many urban gradients extend from agricultural areas to urban areas (all but one, Luck and Wu 2002, of the gradients listed in Table 2) and the general pattern of increasing heterogeneity with increasing urbanization is based on this context. A different pattern emerges when context is not agricultural. Weng (2007) discovered that landscape heterogeneity, as represented by patch density, exhibited a U-shaped pattern along the western half of the gradient: patch density was high in the topographically diverse Driftless Area, low in the urban fringe, and high in the city center (this result is not shown in Table 2). Thus, the context within which an urban area is embedded can affect conclusions regarding urban landscape structure.

The Distinguishing Features of the Study of the Ecology of Urban Landscapes

This section describes the paradigms, subjects of study, and an approach that set the study of the ecology of urban landscapes apart from the study of the ecology of non-urban landscapes.

The gradient paradigm is the dominant conceptual framework used in the study of the ecology of urban landscapes. Approximately 22% of the papers I identified described the investigation of patterns and processes along urban gradients (Table 1). The gradient paradigm has a long and rich history in ecology, with roots in the concept that a continuum might better represent vegetation change over space than discrete classes (Goodall 1963). The gradient paradigm is the view that environmental variables (e.g., soil moisture and elevation) vary continuously over space and that these environmental gradients act to structure ecological communities (Whittaker 1967). McDonnell and Pickett (1990) suggested that the spatial pattern of urbanization, high-density city centers surrounded by irregular rings of decreasing development, could be considered a gradient of environmental variation that could be used to explain variation in ecological patterns and processes. Since McDonnell and Pickett's (1990) seminal paper, at least 300 studies have investigated urban gradients (McDonnell and Hahs 2008). The study of urban gradients has evolved from the investigation of patterns along transects defined by distance from the city center (e.g., McDonnell et al. 1997) to analyses of the multivariate characteristics of a metropolitan region (e.g., Andersson et al. 2009) that more thoroughly describe the complex and indirect nature of the gradient. However, the majority of urban gradient studies, particularly those investigating the distribution of organisms, either define the gradient subjectively (e.g., Blair 1996) or rely on one or a few broad measures of urbanization to characterize it (e.g., Bergerot et al. 2011).

The study of the ecology of urban landscapes is also distinguished from landscape ecological research carried out in non-urban areas by the use of the urban ecosystem paradigm (Table 1). The urban ecosystem has been described as a representation of the Machlis et al. (1997) human ecosystem structured by hierarchical patch dynamics within a watershed (Pickett et al. 1997), as a concept that integrates ecological and social systems in urban areas, also with a theoretical basis in hierarchical patch dynamics (Grimm et al. 2000; Grimm and Redman 2004), and as a complex adaptive system in which biogeophysical and socioeconomic components are grouped as drivers, patterns, processes, and effects or changes (Alberti et al. 2003). A commonality of these formulations is the incorporation of explicit linkages among socioeconomic and biogeophysical variables. The investigation of these linkages is represented in the study of the ecology of urban landscapes by research that relates measurements of income, education level, neighborhood age, immigration status, and unemployment rate, among other variables, to the distribution of vegetation (Kirkpatrick et al. 2007, 2011; Luck et al. 2009; Martin et al. 2004; Ribeiro and Lovett 2009), avian community structure (Lerman and Warren 2011; Loss et al. 2009), and anuran species richness (Smallbone et al. 2011).

The subjects of study that characterize landscape ecological research carried out in urban areas are, in order of the proportion of the papers reviewed here devoted to them, land use/land cover change over time (27%), the ecological effects of land use type (8%), disturbance (7%), human-made habitats (3%), and the ecological effects of land use pattern (0.4%) (Table 1). The land use/land cover change literature included papers that described change over time (e.g., Esbah 2007), calculated rates of change (e.g., Seto and Fragkias 2005), identified the drivers of change (e.g., Gustafson et al. 2005), estimated the ecological impacts of land use/land cover change (e.g., Robinson et al. 2005), or simulated past and future change, typically with the use of cellular automata models (Sante et al. 2010).

The ecological effects of land use type have been investigated at a variety of spatial scales using different conceptual frameworks. Common is the comparison of sites dominated by different land uses within a metropolitan region. For example, Maurer et al. (2000) compared the flora of parks, residential areas, and wastelands formerly occupied by the Berlin Wall in Potsdam and Berlin, Germany. The ecological effects of land use type have also been investigated by comparing landscapes with differing contexts. For example, Gagné and Fahrig (2007) compared anuran community structure in focal ponds surrounded by landscapes dominated by urban, agricultural, or forested land cover. Finally, land use type may be used as a surrogate for matrix type. Kennedy et al. (2010) investigated the effect of matrix type, represented by agriculture, peri-urban development, or bauxite mining, on Neotropical bird community structure in landscapes in central Jamaica.

The study of disturbance in urban landscapes is characterized by a variety of subject matter: fire (e.g., Syphard et al. 2007), tree harvesting (Bhuju and Ohsawa 1999), small-scale disturbances such as windthrow and insect outbreaks that affect individual trees (Litvaitis 2003), air pollution (e.g., Wang and Pataki 2010), the urban heat island effect (e.g., Buyantuyev and Wu 2010), soil heavy metal concentration (e.g., Lin et al. 2002), soil salinity (Miyamoto et al. 2005), metal and metalloid concentrations in Florida scrub-jay (*Aphelocoma coerulescens*) eggs (Burger et al. 2004), disease (e.g., Riley et al. 2007), human presence and trail use (Keeley and Bechard 2011; Miller et al. 2003), predation by domestic cats (*Felis catus*) (e. g., Lepczyk et al. 2004), and traffic noise (Parris and Schneider 2009). This variety is indicative of the suite of changes wrought by urbanization that affect the physical environment and impact ecological systems.

The study of human-made habitats is a less popular but nevertheless distinguishing feature of landscape ecological research carried out in urban areas, perhaps inspired by reconciliation ecology (Rosenzweig 2003). The conservation potential of golf courses (e.g., Colding and Folke 2009) and domestic gardens has attracted particular attention. The latter have been extensively studied in the Biodiversity in Urban Gardens projects, which investigated the spatial distribution of gardens and their environmental and biological characteristics in several European cities (e.g., Loram et al. 2007). Researchers at the University of Tasmania have also conducted several interesting studies on gardens in Australian cities. Kirkpatrick et al. (2007) reported that garden-type prevalence in the suburbs of Hobart was the result of social drivers such as education level and household income and that garden types responded idiosyncratically to these drivers. Daniels and Kirkpatrick (2006) found that the floristic attributes of gardens in Hobart have larger effects on bird community composition than environmental (e.g., altitude) and landscape (e.g., distance to the city center) predictors. Bird species richness and the abundances of individual bird species and groups of species responded idiosyncratically to the floristic composition of gardens. These relationships suggest that private gardens can be designed and managed to promote use by particular bird species or assemblages. More recently, Kirkpatrick et al. (2009) compared the spatial contagion of garden characteristics in Hobart, Australia, to that in Montreal, Canada, and found that, unlike Montreal, adjacent gardens in Hobart did not possess similar attributes.

Finally, a handful of studies have described the ecological effects of residential development pattern. Kleppel et al. (2004) compared the biomasses of emergent vascular plants, phytoplankton, and zooplankton between wetlands situated in watersheds dominated by traditional small-town development (i.e., compact development) or suburban development (i.e., dispersed development) in the Hudson River Valley of New York State, USA. Lenth et al. (2006) compared bird, mammal, and plant communities among clustered developments, dispersed developments, and undeveloped prairie in Colorado, USA. Neither study found significant differences in algal or animal communities between development patterns. Gagné and Fahrig (2010a, 2010b) found that a hypothetical compact development scenario minimized the negative impacts of a given human population on forest biodiversity compared to a dispersed development scenario. Gagné and Fahrig's (2010a, 2010b) work is the only example of a comparison between residential development patterns in which landscape size and the number of dwellings have been controlled.

An approach that promises to yield much insight into the ecology of urban landscapes and is characteristic of landscape ecological research carried out in urban areas is the use of citizen-generated data. Data collected by urban residents, by their sheer number, have the potential to significantly transform the study of urban landscapes (Cooper et al. 2007). Ryder et al. (2010) used data collected as part of the Neighborhood NestWatch project to study nest survival of common songbirds in Washington, DC, USA. They reported that citizen-generated data were of comparable quality to that produced by professional scientists. Weckel et al. (2010) used the innovative approach of distributing surveys via school children as part of a voluntary class assignment to collect the data necessary to model the probability of human–coyote interactions in suburban residential areas in the New York metropolitan region, USA. The model successfully predicted an independent set of data. The authors highlighted the possibility of generating a large amount of data over a large geographic area in a short period of time using citizen science. Such approaches are likely to become more commonplace in the future.

The Ecology of Urban Landscapes

Urban landscapes are heterogeneous and dynamic. They are composed of a multitude of interspersed land use and land cover types, and patterns of land use and land cover may change rapidly over time. Urban landscapes are also dominated by disturbance to physical and biological systems. In this section, I briefly discuss how these characteristics shape the ecology of urban landscapes.

Legacy effects of prior land use/land cover change may persist for decades in urban landscapes. For example, the land use history of the 20th century influences the present-day urban flora in Berlin, Germany (Zerbe et al. 2003). Urban parks established between

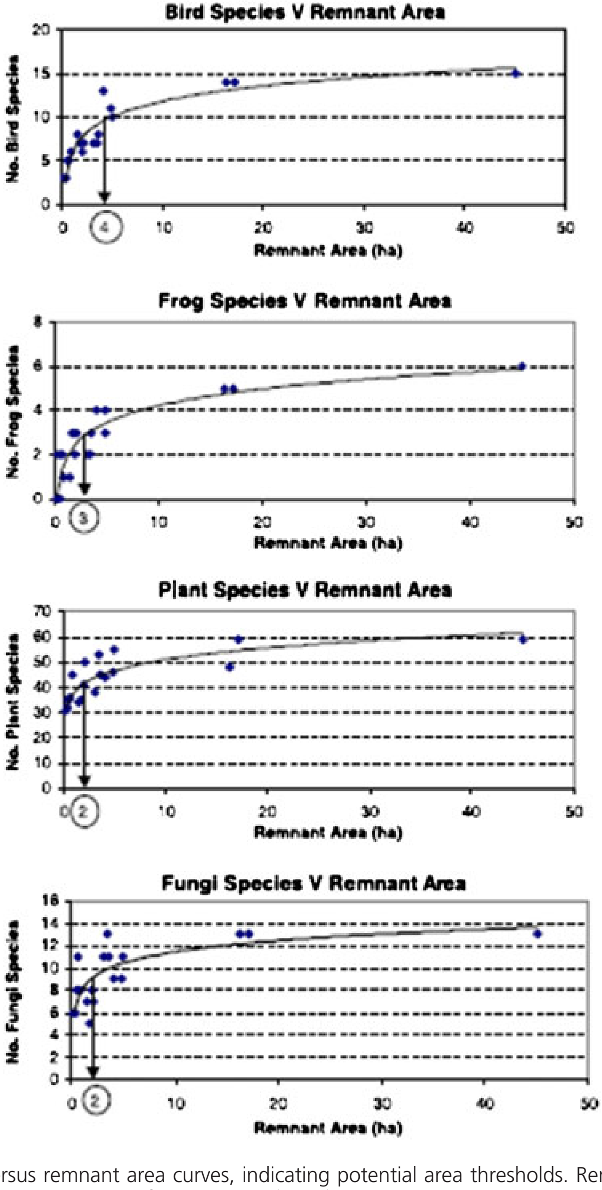

Fig 4. Species richness versus remnant area curves, indicating potential area thresholds. Remnants were located in a suburb of Sydney, Australia. Reproduced from Drinnan (2005) with permission.

the 18th century and the 1970s in Bangalore, India, differ in tree species diversity, tree size class diversity, and tree composition from parks established since 1990 (Nagendra and Gopal 2011). Development age affects bird abundance and species richness (Filippi-Codaccioni et al. 2008; Miller et al. 2003) and anuran relative abundance (Gagné and Fahrig 2010c). Time lags may also occur in urban landscapes. For example, Löfvenhaft et al. (2004) described a lag of several decades between urban intensification and changes in amphibian occurrence in Stockholm, Sweden.

Habitat loss and fragmentation cause significant changes to ecological populations and communities in urban landscapes. Numerous studies have investigated patterns of species occurrence, abundance, and richness in remnant habitat fragments in an urban matrix. Fragment area has generally been found to have a larger effect on species occurrence and richness than fragment isolation (Bräuniger et al. 2010; Drinnan 2005; Fernández-Juricic 2004; Huste et al. 2006; Stiles and Scheiner 2010; Williams 2011). A threshold in fragment area may exist in urban landscapes, below which species richness declines rapidly (Figure 4). The habitat quality of fragments is also an important predictor of community structure (e.g., Fernández-Juricic 2004), sometimes more so than fragment area and isolation (Jellinek et al. 2004).

The quality of the urban matrix surrounding fragments influences community structure in fragments. Matrix quality effects may be manifested in several ways. First, matrix quality may affect species movement among fragments. For example, bandicoot (*Isoodon macrourus*) presence in fragments in Brisbane, Australia, is a function of the estimated resistance to movement of the intervening urban matrix (FitzGibbon et al. 2007). Second, matrix quality may influence resource availability by providing complementary or supplemental resources to those in fragments. Nominal habitat specialists found in exurban and suburban areas are indications of this mechanism at work (Figure 5). Third, matrix quality may mediate edge effects in fragments. The degree of structural contrast between fragment habitat and the matrix can influence microclimate, biotic composition, and ecological functioning within fragments (Harper et al. 2005). For example, Hodgson et al. (2007) compared bird crossings at the edges of remnant bushland fragments abutting areas of low or high housing density in a suburban landscape. Feeding guilds differed in their propensity to cross edge types, and the structure of the vegetation within the

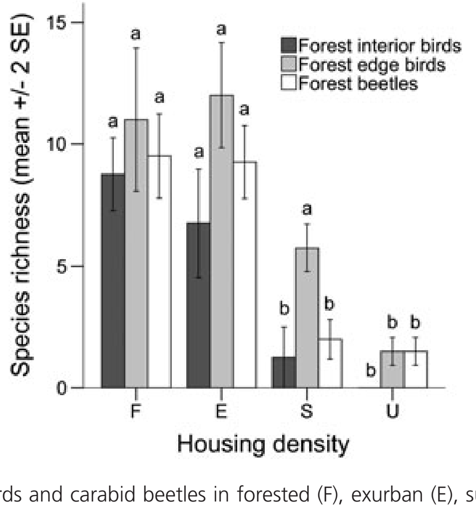

Fig 5. The species richness of birds and carabid beetles in forested (F), exurban (E), suburban (S), and urban (U) sites representing a gradient of increasing housing density. Different lowercase letters above bars indicate significant ($p \leq 0.05$) pairwise differences between site categories for each taxon and habitat affinity group. No significant difference in nominal forest interior bird species richness between forested and exurban sites was found. Reproduced from Gagné and Fahrig (2011) with permission.

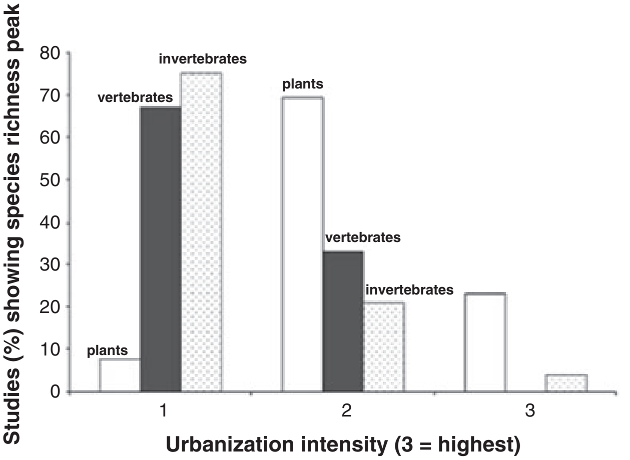

Fig 6. The percentage of urban gradient studies, by taxonomic group, showing species richness peaks at three levels of urbanization (1 = lowest level, 3 = highest level of urbanization). Reproduced from McKinney (2008) with permission.

matrix, such as canopy cover, influenced these trends. Fourth, the occurrence, frequency, and intensity of disturbances in fragments may be altered by matrix quality. For example, human trail use correlates positively with housing density surrounding riparian areas situated along an urban gradient in Colorado, USA, and significantly affects the richness of bird species that forage near the ground in those areas (Miller et al. 2003).

Urban intensification results in major shifts in ecological community structure in urban landscapes. Species richness generally declines with increasing urban intensity, particularly for animals (Figure 6). Peaks in bird and butterfly species richness at intermediate levels of urbanization (Blair 1996; Hogsden and Hutchinson 2004) are notable exceptions to this trend. Plant species richness tends to peak at moderate levels of urban intensity (Figure 6). The intermediate disturbance hypothesis (Connell 1978), a peak in landscape heterogeneity at intermediate levels of urbanization (Porter et al. 2001), and increasing non-native species richness with increasing urban intensity (McKinney 2008) have been suggested as causes of humped-shaped patterns of species richness with respect to urban intensity.

Changes to bird communities with increasing urban intensity have been extensively studied. Bird communities in high-intensity urban areas are characterized by low species richness and a high degree of dominance by a few species (Gagné and Fahrig 2011). Urban intensification also results in the taxonomic and functional homogenization of bird communities (Devictor et al. 2007; Sorace and Gustin 2008) and may filter bird communities on the basis of species traits. For example, Croci et al. (2008) found that bird species that bred in town centers were sedentary, omnivorous, and widely distributed, had large wingspans, and nested more than 5 m from the ground. However, it is important to remember that these patterns of change in bird community structure in response to increasing urban intensity may not be shared by other taxa (Gagné and Fahrig 2011).

Ecosystem functioning varies among land use types in urban landscapes. In the Phoenix metropolitan region, urban land uses are characterized by higher soil inorganic nitrogen concentration, higher abundance of nitrogen stable isotopes (^{15}N) and higher water and organic matter content, as well as increased aboveground net primary productivity and increased plant gas exchange compared to desert sites (Buyantuyev and Wu 2009; Jenerette et al. 2006; Martin and Stabler 2002; Zhu et al. 2006). Vegetation growth in urban land uses in Phoenix is driven by anthropogenic inputs of water and nutrients, overriding the existing relationship between plant growth and precipitation in arid systems (Buyantuyev and Wu 2009). However, urban atmospheric conditions may also play a role. In a simulation experiment, Shen et al. (2008) predicted that the increased temperature, increased CO_2 concentration, and increased nitrogen deposition typical of the Phoenix metropolitan region would result in increased aboveground net primary productivity and soil organic matter content in desert remnants.

Other metropolitan regions exhibit similar patterns of variation in soil properties and processes as Phoenix. Along a New York urban gradient, urban forest soils have higher organic matter concentration than suburban and rural forest soils (Pouyat et al. 2002). In the Baltimore metropolitan region, USA, soils in urban forests have larger NO_3^- pools, higher nitrification rates, higher CO_2 emission rates, and lower rates of uptake of atmospheric CH_4 than soils in non-urban forests (Groffman et al. 2002, 2006). In addition, land use types in Baltimore differ in soil organic carbon density. Low-density residential and institutional land uses have approximately 40% higher organic carbon densities than the commercial land use type (Pouyat et al. 2002). In Fort Collins and the metropolitan region of Denver–Boulder in Colorado, USA, soils of urban lawns have lower rates of uptake of atmospheric CH_4 and greater NO_2 emission rates and store more carbon than soils of native grasslands (Golubiewski 2006; Kaye et al. 2004).

Interestingly, birds may represent a more important vector of nutrient transport in urban than in forested landscapes. Input of nitrogen and phosphorus by crow (*Corvus corone* and *Corvus macrorhynchos*) feces was significantly higher in forests in an urban landscape than in sites in a forested landscape, particularly for roost sites in the urban landscape (Fujita and Koike 2009). In urban roost sites, crows contribute 2.7 times the amount of phosphorus originating off-site and 0.66 times the amount of nitrogen originating off-site than are contributed via other pathways.

Vegetation phenology is altered in urban landscapes compared to non-urban landscapes. The urban heat island effect, higher air temperatures in urban areas than in surrounding rural areas, is associated with earlier vegetation green-up and flowering and a longer growing season in urban areas (Neil et al. 2010; Roetzer et al. 2000; White et al. 2002; Zhang et al. 2004a, 2004b). Zhang et al. (2004b) further showed that an urban climate's footprint is 2.4 times the area of that of urban land use for cities in eastern North America. This means that urban climate influences vegetation phenology in surrounding rural areas, up to 10 km beyond the edge of urban land use. A recent study of the Phoenix metropolitan region reported different results to those described above (Buyantuyev and Wu 2012). It appears that urbanization may lead to a greater diversity of phenological patterns and the decoupling of urban vegetation phenology from climatic drivers. Buyantuyev and Wu (2012) suggested that the high diversity of managed plant communities in urban areas, in terms of their evolutionary histories and physiologies, and human-derived water and nutrient subsidies could be responsible for these patterns.

Variation in ecosystem functioning among land uses in urban landscapes should result in concomitant variation in the provision of ecosystem goods and services. As expected, Dobbs et al. (2011) found that the majority of the indicators of ecosystem goods, services, and disservices that they estimated in Gainesville, Florida, USA, varied among land use types (Table 3).

Future Directions for the Study of the Ecology of Urban Landscapes

Landscape ecological research in urban areas is a relatively new endeavor. Despite this, several distinguishing features, such as paradigms, subjects of study, and an approach, that set it apart from the remainder of the field can be identified (Table 1). Landscape ecologists who study

Table 3. Ecosystem goods, services, and disservices and their indicators in Gainesville, Florida, USA.

Service or disservice	Indicator
Maintenance of air quality	CO_2 sequestration by trees
	Air pollutant removal by trees
Maintenance of favorable climate	Temperature reduction caused by trees
Storm protection	Tree structure
	Crown dieback
Drainage	Curve number
	Soil infiltration
Maintenance of soil quality	Soil fertility
	Soil bulk density
Maintenance of healthy soils	Soil nutrients
	Heavy metals
Filtering dust particles	Pm_{10} removal by trees
	Leaf area and distance to roads
Noise reduction	Type of foliage
Maintenance of biological and genetic diversity	Shannon diversity and evenness index
	Ratio of native trees
Productivity	Tree biomass
Recreation	
Aesthetic	
Disservice	Fruit fall from trees
	Allergenicity
	Damage to infrastructure and risk to human safety from trees
	Decrease in air quality due to emissions from tree pruning and lawn mowing

Indicators of the maintenance of air quality, the filtering of dust particles, and disservices were the only variables that did not vary significantly ($p \leq 0.05$) among land use types. Reproduced from Dobbs et al. (2011) with permission.

urban landscapes use the gradient paradigm and the urban ecosystem framework to shape their research questions. They study subjects such as land use/land cover change, the ecological effects of land use type and pattern, and human-made habitats that receive less attention from landscape ecologists studying non-urban areas. They also study a very wide variety of disturbances that occur in urban landscapes. And, increasingly, they are making use of citizen-generated data to answer their questions. Knowledge of the ecology of urban landscapes is largely based on comparisons of land use types, investigations along the urban gradient, and research centered on remnant habitat fragments in an urban matrix.

In future, there is much topical breadth to be explored in the study of the ecology of urban landscapes. Sixty percent of the 894 papers I reviewed described land use/land cover change over time, quantified landscape structure without investigating the interactions among landscape structure and abiotic and biotic patterns and processes, and/or investigated patterns and processes along urban gradients (Table 1). Many topics that are very common in the landscape ecological literature as a whole, such as island biogeography and connectivity, are very uncommon in the study of the ecology of urban landscapes. This presents landscape ecologists studying urban areas with the opportunity of testing whether understanding derived in less modified landscapes can be applied to intensively modified urban landscapes. Understanding of the functioning of different landscape systems (e.g., agricultural, urban, or forested) might be integrated into a conceptual human modification framework, as envisioned by Forman and Godron (1986). Such a framework could be used to inform the planning and management of regions that encompass a variety of sub-systems. In addition to these endeavors, landscape ecologists studying urban areas should focus their efforts on a second strand of research that is poorly represented presently in the study of the ecology of urban landscapes, that of the interactions between agents of global change, such as climate change, and urbanization (Table 1). Urbanization generally has large effects on abiotic and biotic patterns and processes. The conditions under which these effects will be lessened or magnified by exogenous factors such as climate change will be of major importance in the coming decades for biodiversity conservation and human society.

Notwithstanding these lacunae in the present literature, I foresee three future directions for the study of the ecology of urban landscapes. First, fragmentation research in urban landscapes should increasingly focus on matrix quality and its effects on the biodiversity of habitat fragments. Many urban areas are of low to moderate intensity, such that they contain a mix of human land uses and remnant habitat (i.e., Forman and Godron's, 1986, suburban landscapes). The fragments in these areas have enormous conservation potential. To date, the majority of research on the biodiversity of fragments in urban landscapes has ignored matrix quality despite the likelihood that it has a large effect (Fahrig 2001). Future research should focus on the relative effects of habitat loss, habitat fragmentation *per se*, and urban matrix quality at the landscape scale (*sensu* Fahrig 2003). The urban gradient may be a useful approximation of matrix quality in these investigations (e.g., Brady et al. 2011). Future research should also focus on the underlying mechanisms by which matrix quality affects biodiversity in fragments. To date, most attention has been paid to the influence of matrix quality on species movement among fragments. Surprisingly little attention has been paid to edge effects in urban landscapes, despite the high edge density of these areas (Table 2).

Second, the study of the ecology of urban landscapes should shift its focus from comparisons of different land use types to investigations of the ecological effects of different land use patterns. In this paper, I described the results of four studies that compared compact and dispersed residential development patterns. Many more studies are needed to fully investigate the ecological effects of building compact and dispersed residential developments and of differing patterns of urban land uses in general. Land use pattern may significantly affect the provision of ecosystem goods and services in urban landscapes, with implications for urban planning and design.

Ultimately, the study of the ecology of urban landscapes should take into account the trade-offs between human needs and the needs of other species (Hostetler 1999), which is the third future direction of study I foresee. For example, Gagné and Fahrig (2010a, 2010b) showed that the species richness of forest breeding birds and forest ground beetles was highest in a hypothetical landscape with compact rather than dispersed development because the former contained a large area of continuous forest cover. However, Cho et al. (2009) found that smaller forest patches in urbanizing areas of the Southern Appalachian Highlands, USA, were associated with higher housing prices. Which of these results should carry more weight if the goal is sustainability? Wu (2010) asserted that "urban sustainability, . . ., has become an inescapable goal of landscape ecology." To achieve this goal, the study of the ecology of urban landscapes should increasingly focus on transdisciplinary research. Collaborations between natural and social scientists, among others, are the only means by which questions about urban landscapes that will have long-term relevance to human society can be answered.

In conclusion, it is clear from the existing research on the ecology of urban landscapes and future avenues of study that the discipline offers the promise of discoveries, surprises, and ultimately, one hopes, a sustainable urban future.

Short Biography

Sara A. Gagné completed her Ph.D. at Carleton University in Ottawa, Canada. Before joining the Department of Geography and Earth Sciences at the University of North Carolina at Charlotte as an assistant professor, she held the position of research associate for a year in the Department of Forest and Wildlife Ecology at the University of Wisconsin–Madison. Her research, teaching, and outreach activities are focused on urban biodiversity conservation. Most notably, she has investigated the effects of urbanization on anuran community structure and assessed the effect of the housing density/sprawl area trade-off on forest biodiversity. She is currently researching the distribution of carabid beetles at urban forest edges and the provision of ecosystem services by green roofs.

Note

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