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Ecological concepts necessary to the conservation of biodiversity in urban environments

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Invited Paper

Abstract:
Increasingly, landscape architects, planners and other land-use practitioners have the task of creating functional landscapes that maintain biodiversity. They need to be familiar with a range of evolving concepts and techniques that have been identified as crucial in the conservation of biodiversity. We discuss key concepts, eg. island biogeography, minimum viable populations, metapopulations, homogenization, extinction debt, and patch dynamics, which link species richness to biodiversity at the regional scale. We use birds as a scaling example to demonstrate the range of research necessary to assess biodiversity across multiple scales in an urban environment.

Introduction

Urbanization is an extreme form of land use. Urban land cover is positively correlated with species richness and endemism (Myers et al. 2000). Urban areas threaten ecosystems: directly, through habitat conversion, and indirectly, through habitat fragmentation. Fragmentation occurs when once continuous habitats are divided into separate fragments (Hanski 1999). Human-associated fragmentation causes biodiversity decline because it destroys species (Ehrlich and Ehrlich 1981), disrupts community interactions (Wilcox and Murphy 1995), and interrupts evolutionary processes (Levin 1999), resulting in irreversible losses of biological diversity (Olff and Ritchie 2002, Wackernagel et al. 2002).

An ecosystem can be compared to a tapestry of species and relationships. Quammen (1996) takes an imaginary Persian carpet and cuts it into pieces, then measures the total area of the fragments, and asks whether we now have several nice Persian throw rugs. Sadly, the answer is no. Rather, the remains are ragged fragments, worthless and commencing to come apart. What we know about the process of fragmentation and what goes on within the remaining patches is vital to our understanding of how to piece together the tapestry of biodiversity. If our regional tapestries of ecosystems, habitats, and species are not to come apart at the seams, green structure and sustainability need to be intimately linked in the planning process (Bergen Jensen et al. 2000).

In the wake of the United Nations Conference on Environment and Development (UNCED 1992), initial estimates of changes in land use and land cover attributable to human settlement were undertaken (eg. Douglas 1994). Estimates of the fraction of land transformed or degraded by humanity were calculated to be as much as 50% (Vitousek et al. 1997). Because land that has not been transformed has often been divided into fragments by human alteration of the surrounding areas, even this figure may understate the problem.

Human overpopulation globally has been linked with habitat loss (Heywood 1995) and associated land transformation the primary source of loss of biological diversity worldwide (Wackernagel et al. 2002). The effects of land transformation extend far beyond the boundaries of transformed land directly affecting the species composition and functioning of otherwise little modified ecosystems and climate at the regional scale (Olff and Ritchie 2002). In short, land transformation is causing irreversible losses of biological diversity.

Ecology in an urbanizing world

Traditionally, ecologists have worked in relatively large scale pristine environments (Fazey et al. 2005, Cairns 1988, Soulé 1985, Wilson and Willis 1975). The belief was that for the field to progress, research had to focus on natural systems (Grimm et al. 2000). Humans and their institutions were not incorporated into studies of ecology (McDonnell and Pickett 1990). Research on the association of biodiversity and urban ecosystems was concerned with the impact of urbanization on biodiversity (Rebele 1994). The recognition that humanity dominated the Earth’s ecosystems (Vitousek et al. 1997) was critical in re-orienting ecologists toward the urban ecosystem itself.

In 1900, only 14% of the world’s population lived in urban communities (Douglas 1994). In 1975 that figure was 38%, in 1995 it had risen to 45%, and in 1999 it had reached 47%. The United Nations (UNPD 2006) revised population estimate for 2005 projects an urban population of 52.9% in 2015. The World Resources Institute (WRI 1997) has projected that 61% of the world’s population will be urban by 2025. Over 90% of that growth will occur in developing cities (UNCHS 1996). Those cities which are predicted to see the most urban growth are to be found in the world’s biodiversity hotspots (McKee et al. 2003, Cincotta et al. 2000).

The biodiversity hotspots are 25 areas from across the globe (Myers 1988) that are especially rich in endemic species and particularly threatened by human activities. Having estimated key demographic variables for each hotspot, Cincotta et al. (2000) reported that in 1995 nearly 20% of global population was living within the hotspots, an area covering about 12% of Earth's terrestrial surface. They determined that the 1995-2000 annual population growth rate in the hotspots was 1.8%, substantially higher than the 1.3% world average. It was even above the annual average of 1.6% for developing countries. Substantial human-induced environmental changes are linked to urbanization at a regional scale (Haines-Young 2000) and will remain an important factor in global biodiversity conservation (Cincotta et al. 2000, Rebele et al. 1994, Kates et al. 2001).

Twentieth-century urban form in North America and Europe has an intensively developed core surrounded by irregular rings of diminishing levels of development. Environmental variation, such as species richness or habitat diversity, is ordered in space along a gradient moving from the core to the periphery. Urban gradient analysis attempts to capture this gradient of environmental variation and to examine the response of the biotic community (McDonnell and Pickett 1990). Most studies investigating biodiversity within cities have used a gradient approach (eg. Small et al. 2006, Williams et al. 2005, Crooks et al. 2004, Maestas et al. 2003, Porter et al. 2001, Medley et al. 1995, McDonnell and Pickett 1990). They usually show a correlation between the number of species and the diversity of land use patterns encountered moving from the city center to the outskirts of the city. The greatest variety of land use patterns can be found in the transition zone between the city center and the outskirts where urban structures are closely associated with open spaces like large parks, urban forests, and larger ex-urban areas (Walmsley 1995, Alberti 2005, DeStefano and DeGraaf 2003).

Genuine interest in the ecological functioning of urban areas has coincided with the realization that we had become an urban species (Folke et al. 1996, Slocombe 1993). However, research on biodiversity conservation in urban environments has largely overlooked new urbanizing forms and polycentric cities, eg. Bangkok, Istanbul, Sao Paulo, where most of the world’s urban growth is taking place. Massive changes are taking place in the size, extent and nature of urban settlements (Champion and Hugo 2004). In particular, these changes have involved a blurring of the urban-rural distinction. Frequently, there is no longer a clear dividing line between town and countryside. There now exists a wide array of alternative forms of development whose extensive spatial units include extended metropolitan regions, functional urban regions, daily urban systems, and vast market areas. Although geographers recognized these changes over 40 years ago (Gottman 1961), apart from a few exceptions (eg. Marzluff et al. 2001), they have yet to fully penetrate studies on the conservation of biodiversity in urban settings (eg. Crooks et al. 2004, Melles et al. 2004, Maestas et al. 2003, Blair 1999). To capture the increasing complexity of human settlement patterns regional level biodiversity conservation strategies that incorporate a multi-scale view of biodiversity will have to become the norm (eg. Blair 2004, Elmqvist et al. 2004, Dale et al. 2000, Allen and O'Connor 2000).

The importance of regional scale for biodiversity conservation

Cities are maintained for centuries in a disequilibrium state from the local natural environment by the importation of vast resources of energy and materials. By making traditional ecological footprint analysis (Wackernagel and Rees 1996) spatially explicit, Luck et al. (2001) were able to capture the urban ecosystem pattern and process of resource appropriation and waste generation at multiple spatial scales. They described the complex interactions occurring across multiple scales as characteristic of urban ecosystems. Another approach to studying urban landscapes was the spatially focused approach of patch dynamics introduced by Wu and Loucks 1995). Their approach laid the groundwork for later research which showed that the interactions between an urban settlement and the natural environment which occur at either a local or regional spatial scale, depending on size and density (Bessey 2002), require a large-scale spatial structure of heterogeneous ecosystems to conserve biodiversity in human-dominated landscapes.

In the earlier stages of research, basic questions related to whether or not a theory of urban ecology was necessary (Niemelä 1999a, Botkin and Beveridge 1997) and, if so, how ecology and urban planning could be interconnected (Alberti 2005, Niemelä 1999b). The main reasons for the lack of a more generalized approach to biodiversity research was the habitat complexity of (sub)urban parks (Gilbert 1989) where the predominance of recreational and ornamental functions (Pysek 1998, Angermeier 1994, Murphy 1988) complicated the research. When it was determined that urban and suburban parks can have high species richness (Boothby 2000), the policy prescription was to focus on the role of urban parks and greenbelts (Boothby 2000, EEA 1997) as a means to shore up urban biodiversity.

Today, we know that green infrastructure is a key issue in urban planning (Yokohari et al. 2000, Sandström 2002). Yet, greenway systems which have sought to limit sprawl have often had the opposite effect. Planning guidance concerned with controlling development by relegating formal nature conservation to designated areas, partly a result of the widespread belief that the urban landscape is categorically distinct from its ecological surroundings, have resulted in large semi-natural parks and set-asides on the periphery of urban environments draw upon both financial and spatial resources where both are in short supply. In this scenario environment, ecosystems, habitats, became something “out there” to be protected and conserved (Pezzoli 2000). Rather, the city itself, must be seen as the central figure in the landscape and greenway planning is the means by which to link urban areas and the surrounding countryside in a hierarchy of local, regional, and national areas (Fábos and Ryan 2004, Bryant 2006) in which biodiversity is appropriately nested.

The term biodiversity generates misunderstanding

Since the term “biodiversity” transcends all levels of life from genes to communities and all spatial and temporal scales, it has generated confusion and misunderstanding (Lautenschlager 1997). In simplest terms, biodiversity (biological diversity) is the variety of life and its processes, including the variety of living organisms, the genetic differences among them, the communities, ecosystems, and landscapes in which they occur, plus the interactions of these components (West 1993), namely, their structural and functional attributes (Forman and Collinge 1997, Noss 1992). Levels of biological organization often correspond to specific spatial and temporal scales (Scott et al. 2002, Fernández-Juricic and Jokimäki 2001).

Biodiversity, then, is an interlocked hierarchy of elements on several levels of biological organization (Noss, 1992), a concept known as “nested hierarchy”. The multiscale content of biodiversity means that concerns can occur at any level of organization and, therefore, need to be addressed at their appropriate scale (Bessey 2002). From the perspective of landscape ecology, biodiversity is composed of three interlocking elements that are central to the planning process. They are the compositional, structural, and functional elements of an ecosystem (Noss 1992, Forman and Godron 1992). Components such as species are linked with structure such as habitat diversity, which in turn is often dependent on the function of natural processes for its renewal (Sandström et al. 2006a).

Within patch diversity has tended to focus on species richness in urban and suburban parks (eg. Hermy and Cornelis 2000). Most often it is restricted to a specific species group, for example, vascular plants (Weifeng et al. 2006, Zerbe et al. 2004, Chocholousova and Pysek, 2003), trees (Jim and Chen 2003, Medley et al. 1995), bats (Kurta and Teramino 1992), arthropods (McIntyre et al. 2001, Natuhara et al. 1994), carabid beetles (Woodward et al. 2003), butterflies (Wood and Pullin 2002), amphibians (Parris 2006, Rubbo and Kiesecker 2005, Carr and Fahrig 2001), small mammals (Andrén 1994, Nilon and VanDruff 1987) or birds (Crooks et al. 2004, Fernández-Juricic 2001).

Fragmentation is the act of making islands
McArthur and Wilson (1967) developed the theory of island biogeography in the context of the flora and fauna of real islands which they interpreted as a balance between the opposing forces of extinctions and colonizations. Fragmentation is the act of making islands because it causes an interruption in the spatial distribution of land, resulting in the loss of habitat and habitat patch isolation giving patches in the landscape many of the properties of true islands. In an urban environment, the built environment becomes the sea surrounding isolated patches of green.

Within the rubric of island biogeographic theory are the two most important processes determining the abundance of organisms (Taylor 1990): the habitat patch and the dispersal distance between patches. In biodiversity research this translates into the species-area relationship (Simberloff 1988) and metapopulation dynamics (Doak and Mills 1994). Habitat loss decreases population sizes and increases extinction rates through inbreeding depression, stochastic extinction, or just breeding down to zero (Akçakaya and Sjögren-Gulve 2001), and isolation decreases the likelihood of recolonization of otherwise productive habitat (Hanski and Ovaskainen 2000).

Tilman et al. (1994) used the term “extinction debt” to describe the local extinction of species and populations through the preferential loss of competitive species following a prolonged transient or delay following habitat destruction. Loehle and Li (1996) showed that even in larger framents of remnant vegetation an extinction debt occurs due to gradual stochastic elimination of species that are very rare and isolated in these fragments. Within urban landscapes, different types of green space are a major limitation to both species richness and viable populations (Fahrig, 2002).

The number of individuals in a given population is always fluctuating due to numerous influences, from extrinsic changes in the surrounding environment to intrinsic forces within a species' own genes. This population fluctuation is especially a problem for populations in isolated fragments and species that are critically endangered throughout their range. When a population falls below a certain number, known as the minimum viable population (MVP), it is unlikely to recover (Shaffer 1981). There are three common forces that can drive a species with a population under MVP to extinction: demographic stochasticity, environmental stochasticity, and reduced genetic diversity.

Wilson and Willis (1975) showed that smaller patches were more fragmented than larger patches, single patches were less fragmented than subdivided patches of the same total area, and groups of patches that were closer together were considered less fragmented than further spaced patches. Species richness decreases toward smaller spatial scales. The species–area curve has been extensively investigated by ecologists (Tjorve 2003). The species–area curve can differ strikingly depending on which taxonomic or functional group is being studied. Biological diversity or, species richness, depends on differences in the age of the island, the size of the island, and differences in the rate of immigration and extinction (Fangliang and Legendre 1996, McGuinness 1984).

At a larger scale, within-patch diversity is linked to a metapopulation (Levins 1969), a concept introduced to describe a subdivided patchily distributed population in which the population dynamics operates at two levels, within and between patches (Cornelis and Hermy 2004). A metapopulation exists as a series of sub-populations linked by migration between isolated patches (Pulliam 1988). Equilibrium metapopulations are well mixed and interconnected by dispersal so they function essentially as a single population. Local extinctions are recolonized immediately, and a single individual might live in multiple patches during its lifetime. In island biogeographic cases, the mainland (or source) population is resistant to extinction while an island (or sink) population tends to go extinct repeatedly and be recolonized by dispersal from the mainland source. Fragmentation results in the development of non-equilibrium meta-populations in urban environments (Harrison and Bruna 1999, Hanski 1994) because when individuals are not able to disperse and colonize other patches the result is local extinction (Hanski and Simberloff 1997). By definition, the mainland is persistent, so by implication, the metapopulation is too. However, in today’s urbanizing environment there often is no mainland, only islands of varying size and condition.

However, the issue of whether one large or several smaller reserves was best had been a long standing topic of investigation in conservation biology. While the full implications of fragmentation had been revealed, there was no agreement on what an adequately large reserve would be (Wilcox and Murphy 1995). It is from this uncertainty that the question of maintaining overall versus selective regional diversity has arisen and the role of corridors has given over to that of networks (Opdam et al. 2006, Linehan et al. 1995, Walker 1992). A sufficiently well-connected network of habitats, which varies for different groups of species (Angelstam et al. 2004), is crucial to maintaining biodiversity.

Twenty years of research on fragmentation had demonstrated its central role in reducing population size based on the loss of linkages or connectivity between habitat patches (Beier and Noss 1998). Forman and Godron’s (1986) patch-corridor-matrix model re-stated the theory of island biogeography by focusing explicitely on the spatial dynamics of the patches in which variation in patch size, shape, location, and quality are considered relevant variables. During the 1990s, re-establishing connectivity between patches became an integral part of both the research (Collinge 1996) and planning (Ahern 1996) agenda.

Homogenization

When measured by extent and intensity, urbanization is one of the most homogenizing of all major human activities (McKinney 2006). As cities expand biological homogenization increases (Olden et al. 2006, McDonnell and Pickett 1990) with the same species becoming increasingly widespread and locally abundant in cities throughout the world. Initially, biodiversity in urban fragments mimics biodiversity in the surrounding region (Clergeau et al. 2001). However, it changes over time in a predictable manner (Olden et al. 2006). Green space development that concentrates on the physical environment, clean air and water, or nominally on park areas, fails to consider the configuration, juxtaposition, and functional relationships between green patches as an essential component of an ecologically sound approach to development (Forman and Godron, 1986). Ensuring long term integrity of biodiversity within a broader landscape context will depend on creating and maintaining functional and spatial connectivity and buffer areas.

Evidence for the loss of biodiversity from urban parks is now conclusive. The proportion of non-native plant species in human settlements always increases through time (McKinney 2006). New York City has lost 578 native species (a loss of roughly 43% of the original native species) while gaining 411 non-native species (DeCandido et al. 2004). Similarly, in the last century, Needham, Massachusetts has lost over 330 native plant species (about 44% of its native richness) while gaining over 200 non-native species (Standley 2003). Drayton and Primack (1996) demonstrated that Boston Common had lost 155 species within a century. European cities also show this trend (Van der Veken et al. 2004). In the last 120 years, the city of Plzen in the Czech Republic lost 368 native species (about 31%) while gaining 238 non-native species (Chocholouskova and Pysek 2003). In Adelaide, Australia between 1836 and 2002, at least 89 species of native plants disappeared and 613 non-native species were added (Tait et al. 2005).

There is a clear trend of an increasing proportion of non-native species toward the urban core. Urban–rural gradient studies have provided important insight into associations between urbanization and biotic homogenization across a range of organisms, eg. avifauna (Marzluff 2001), mammals (Baker et al. 2003, Dickman and Doncaster 1987), carabid beetles (Small et al. 2006), butterflies (Wood and Pullin 2002), and arthropods (McIntyre 2001).
Invasive species can accelerate the process of homogenization (McKinney 2006, McKinney and Lockwood 1999). Parks and gardens are replete with ornamentals and exotic vegetation, but understanding when and how an exotic can become an invasive depended on the development of ecological principles (Lonsdale 1999). Shea and Chesson (2002) offer a useful framework for understanding urban disturbance and invasion by focusing on ‘‘niche opportunity’’. This defines conditions that promote species invasions in terms of three key variables: resources, natural enemies, and the physical environment. An invasion-promoting disturbance increases the population growth of an invading species by providing resources, reducing the threat of natural enemies and/or altering the physical environment (e.g., available radiation, temperature) to improve habitability for the invader (Vitousek 1990). The growing literature of urban impacts on biological communities has used niche opportunities to model invasions (Kolar and Lodge 2001). The direct cost to ecological goods and services that invasives can have by impacting on regional level biodiversity is huge (Pimentel et al. 2000).

Scaling up

Taxonomic biases (Baldi and McCollin 2003, Clark and May 2002) in field studies have resulted in our knowing much more about some species than others. A majority of species-oriented conservation biology involves birds (eg. Sandström et al. 2006b). Birds are the only taxonomic group for which a global assessment of the wide-reaching effects of urbanization exists (Marzluff 2001), they can be used as a surrogate taxa for assessing biodiversity (Fleishman et al. 1999, Blair 1999).

Urbanization has negative impacts on birds (Blair 2004, Mörtberg and Wallentinus 2000, Jokimäki 1999). All species are equal but some are more equal than others (Fleishman et al. 1999). Local endemic species (often urban-sensitive species) are frequently replaced by ubiquitous non-native species (urban-adapted species). An investigation into Beijing inner-city parks revealed that of the 288 species recorded 41% were exotic (Weifeng et al. 2006). Species assemblages show increased similarity within parks of a similar age, eg. development history or landscape design. Crooks et al. (2004) found that as sites become more urban avian assemblages in southern California were progressively more similar to those in northern California and Ohio.

Species vary in size, shape, abundance, distribution, trophic position, ecological function, feeding habits and desirability. Therefore, diversity indices which assume all species as being equal are of little use for properly managing biodiversity (Savard et al. 2000). Several reviews of the various scales at which a species can be assessed across a range of urban land uses have been published (eg. Blair 2004, Jokimäki et al. 2003, Allen and O'Connor 2000). They include the effects of spatial pattern (Fernández-Juricic 2001), habitat fragmentation (Hansson 2000), landscape composition and scale (Blair 2004), community composition (Park and Lee 2000), and the distribution of individual birds within patches (Morneau et al. 1999). Different groups of birds appear to be affected in different ways (Opdam 1991), and this has distinct conservation implications. Not only does urbanization affect the heterogeneity of the landscape and, consequently, the distribution, abundance, and resources upon which birds depend (Melles et al. 2003), but, importantly, bird population declines affect ecosystem processes (Sekerciolu et al. 2004).

Greenway planning and sustainable cities

Implementing regional biodiversity conservation strategies will require new interdisciplinary collaboration to achieve both the biophysical and socio-economic quality of life characteristic of a sustainable future. Several cities have introduced regional planning programs to conserve biodiversity, eg. Baltimore (Pickett and Cadenasso 2006), Chicago (Wang and Moskovitz 2001), New York (Flores et al. 1998). Within Europe, the development of regional level ecological networks has been part of conservation planning for almost twenty years (Bennett 1999, Jongman 1995). The European Environmental Agency has advocated regional landscape planning as an integral component of sustainable development (EEA 1997) culminating in the European Landscape Convention (Council of Europe 2000).

Traditionally, the association of biodiversity and urban ecosystems has been concerned with the impact of urbanization on biodiversity. Today we know that for urban settlements to be ecologically sustainable they need to be part and parcel of the landscape structure that supports the ecological processes required by the landscape to deliver biodiversity services (Opdam et al. 2006). The key is finding complementarity at a regional scale in which a nested hierarchy of diversity is embedded in a human dominated landscape.

Conservation biologists now face the challenge of modeling ecosystem change in urban ecosystems, the surrounding human-dominated lands, and natural areas. To preserve options the functional roles of species and ecosystems, or, put another way, of ecological goods and services, will require increased levels of understanding of ecological principles.

Implementing regional conservation strategies will require new interdisciplinary collaboration to achieve both the biophysical and socio-economic quality of life characteristic of a sustainable future. Complementary and inter-related, cities not only as the cause, but part of the response, to today's biodiversity crisis. The solution is design that enables diversity.

Given the entirely urban character and the limited financial and political resources available for conservation in urban settings, especially in the developing world (Luken 2006), combined with the extreme importance (Myers et al. 2000), even, fragility (Mittermeier et al. 2004), of the resources to be conserved, any framework for conservation needs to focus on long-term ecological sustainability with the proviso that where compositional, structural, and functional attributes do not presently exist, they can be built in over time. Creating such a framework using spatially explicit models and standard landscape ecology patch-corridor principles is a principle task of both landscape ecologists and urban planners.

Literature

Ahern, J., (1996), Greenways as a planning strategy. pp. 131-155 in: Fabos, J. and Ahern, J. (Eds), **Greenways: The beginning of an international movement**. Elsevier, Amsterdam, The Netherlands.

Akçakaya, H., Sjögren-Gulve, P., (2001), Population viability analyses in conservation planning: An overview. **Ecological Bulletin**, Vol. 48, 9-21.

Allen, A., O'Connor, R., (2000), Interactive effects of land use and other factors on regional bird distributions. **Journal of Biogeography**, Vol. 27, 889-900.

Alberti, M., (2005), The effects of urban patterns on ecosystem function. **International Regional Science Review**, Vol. 28, 168-192.

Andrén, H., (1994), Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: A review. **Oikos**, Vol. 71, 355–366.

Angelstam, P., Dönz-Breuss, M.,, Roberge, J.-M., (2004), Targets and tools for the maintenance of forest biodiversity. **Ecological Bulletin**, Vol. 51, 427–453.

Angermeier, P., (1994), Does biodiversity include artificial biodiversity? **Conservation Biology**, Vol. 8, 600–602.

Baker, P., Ansell, R., Dodds, P., Webber, C., Harris, S., (2003), Factors affecting the distribution of small mammals in an urban area. **Mammal Review**, Vol. 33, 95-100.

Baldi, A., and McCollin, D., (2003), Island ecology and contingent theory: The role of spatial scale and taxonomic bias. **Global Ecology and Biogeography**, Vol. 12, 1–3.

Beatley, T., (2000), Preserving biodiversity: Challenges for planners. **Journal of the American Planning Association**, Vol. 66, 5-20.

Beier, P., Noss, R., (1998), Do habitat corridors provide connectivity? **Conservation Biology**, Vol. 12, 1241-1252.

Bennett, A., (1999), **Linkages in the landscape: The role of corridors and connectivity in wildlife conservation**. IUCN, Gland, Switzerland.

Bergen Jensen, M., Persson, B., Guldager, S., Reeh, U., Nilsson, K., (2000), Green structure and sustainability: Developing a tool for local planning. **Landscape and Urban Planning**, Vol. 52, 117–133.

Bessey, K., (2002), Structure and dynamics in an urban landscape: Toward a multiscale view. **Ecosystems**, Vol. 5, 360-375.

Blair, R., (1999), Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? **Ecological Applications**, Vol. 9, 164-170.

Blair, R., (2004), The effects of urban sprawl on birds at multiple levels of biological organization. **Ecology and Society,** Vol. 9, [online] URL: http://www.ecologyandsociety.org/vol9/iss5/art2

Boothby, J., (2000), An ecological focus for landscape planning. **Landscape Research**, Vol. 25, 281–289.

Botkin, D., Beveridge, C., (1997), Cities as environment. **Urban Ecosystems**, Vol. 1, 3–9.

Bryant, M., (2006), Urban landscape conservation and the role of ecological greenways at local and metropolitan scales. **Landscape and Urban Planning**, Vol. 76, 23–44.

Cairns, J., (1988), Restoration ecology: The new frontier. Pp. 2-11 in: Cairns, J., (Ed.), **Rehabilitating damaged ecosystems**. CRC Press, Boca Raton, Florida, USA.

Carr, L., Fahrig, L., (2001), Effect of road traffic on two amphibian species of differing vagility. **Conservation Biology**, Vol. 15, 1071–1078.

Champion, A., Hugo, G., (Eds.), (2004), **New Forms of urbanization: Beyond the urban rural dichotomy**. Ashgate Publishing, Aldershot, England.

Chocholouskova, Z., Pysek, P., (2003), Changes in composition and structure of urban flora over 120 years: A case study of the city of Plzen. **Flora**, Vol. 198, 366–376.

Cincotta, R., Wisnewski, J., Engleman, R., (2000), Human population in the biodiversity hotspots. **Nature**, Vol. 404, 990-992.

Clark, J., May, R., (2002), Taxonomic bias in conservation research. **Science**, Vol. 297, 191–192.

Clergeau, P., Jokimäki, J., Savard, J.-P., (2001), Are urban bird communities influenced by the bird diversity of adjacent landscapes? **Journal of Applied Ecology**, Vol. 38, 1122-1134.

Collinge, S., (1996), Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. **Landscape and Urban Planning,** Vol. 36, 59-77.

Cornelis, J., Hermy, M., (2004), Biodiversity relationships in urban and suburban parks in Flanders. **Landscape and Urban Planning**, Vol. 69, 385–401

Council of Europe, (2000), European Landscape Convention, ETS No. 176.

Crooks, K., Suarez, A., Bolger, D., (2004), Avian assemblages along a gradient of urbanization in a highly fragmented landscape. **Biological Conservation**, Vol. 115, 451–462.

Daily, G., (2001), Ecological forecasts. *Nature*, Vol. 411, 245.

Dale, V., Brown, S., Haeuber, R., Hobbs, N., Huntley, N., Naiman, R., Reibsame, W., Turner, M., Valone, T., (2000), Ecological principles and guidelines for managing the use of land. **Ecological Applications**, Vol. 10, 629-670.

DeCandido, R., Muir, A., Gargiullo, M., (2004), A first approximation of the historical and extant vascular flora of New York City: Implications for native plant species conservation. **Journal of the Torrey Botanical Society**, Vol. 131, 243–251.

DeStefano, S., DeGraaf, M., (2003), Exploring the ecology of suburban wildlife. **Frontiers in Ecology and the Environment**, Vol. 1, 95–101.

Dickman, C., Doncaster, C., (1987), The Ecology of Small Mammals in Urban Habitats. I. Populations in a Patchy Environment. **Journal of Animal Ecology**, Vol. 56, 629-640.

Doak, D., Mills, S., (1994), A useful role for theory. **Conservation Ecology**, Vol. 75, 615-626.

Douglas, I., (1994), Human settlements. Pp. 149-169 in: Meyer, W., and Turner II, B., (Eds.), **Changes in land use and land cover: A global perspective.** Cambridge University Press, Cambridge, UK.

Drayton, B., Primack, R., (1996). Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. **Conservation Biology**, Vol. 10, 30–39.

EEA, (1997), **Towards sustainable development for local authorities: Approaches, experiences and sources**. European Environment Agency, Copenhagen.

Ehrlich, P., Ehrlich, A., (1981), **Extinction**. Oxford University Press, Oxford, England.

Elmqvist, T., Berkes, F., Folke, C., Angelstam, P., Crepin, A., Niemela, J., (2004), The dynamics of ecosystems, biodiversity management and social institutions at high northern latitudes. **Ambio**, Vol. 33, 350-355.

Fábos, J., Ryan, R., (2004), International greenway planning: an introduction. **Landscape and Urban Planning**, Vol. 68, 143–146.

Fahrig, L., (2002), Effect of habitat fragmentation on the extinction threshold: A synthesis. **Ecological Applications**, Vol. 12, 346–353.

Fazey, I., Fischer, J., Lindenmayer, D., (2005), What do conservation biologists publish? **Biological Conservation**, Vol. 124, 63–73.

Fernández-Juricic, E., (2001), Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. **Biodiversity and Conservation**, Vol. 10, 1303–1316.

Fernández-Juricic, E., Jokimäki, J., (2001), A habitat island approach to conserving birds in urban landscapes: Case studies from southern and northern Europe. **Biodiversity and Conservation**, Vol. 10, 2023–2043.

Fangliang, H., Legendre, P., (1996), On species-area relations. **American Naturalist,** Vol. 148, 719-737.

Fleishman, E., Wolff, G., Boggs, C., Ehrlich, P., Launer, A., Niles, J., Ricketts, T., (1999), Conservation in practice: Overcoming obstacles to implementation. **Conservation Biology**, Vol. 13, 450–452.

Fleishman, E., Jonsson, B., Sjögren-Gulve, P., (1999), Focal species modeling for biodiversity conservation. **Ecological Bulletin**, Vol. 48, 85–99.

Flores, A., Picket, S., Zipperer, W., Pouyat, R., Pirani, R. (1998), Adopting a modern ecological view of the metropolitan landscape: The case of a greenspace system for the New York city region. **Landscape and Urban Planning**, Vol. 39, 295-308.

Folke, C., Holling, C., Perrings, C., (1996), Biological diversity, ecosystems, and the human scale. **Ecological Applications**, Vol. 6, 1018– 1024.

Forman, R., Godron, M., (1986), **Landscape ecology**. Wiley, New York, USA.

Forman, R., Collinge, S., (1997), Nature conserved in changing landscapes with and without spatial planning. **Landscape and Urban Planning**, Vol. 37, 129–135.

Gilbert, O., (1989), **The ecology of urban habitats**. Chapman & Hall, London, UK.

Gottmann, J., (1961), *Megalopolis:* **The urbanized northeastern seaboard of the United States**. MIT Press, Boston, MA, USA.

Grimm, N., Grove, J., Picket, S., Redman, C., (2000), Integrated approaches to long-term studies of urban ecological systems. **BioScience**, Vol. 50, 571-584.

Haines-Young, R., (2000), Sustainable development and sustainable landscapes: Defining a new paradigm for landscape ecology. **Fennia**, Vol. 178, 7–14.

Hansson, L., (2000), Edge structures and edge effects on plants and birds in ancient oak-hazel woodlands. **Landscape and Urban Planning**, Vol. 46, 203–207.

Hanski, I., (1994), Patch-occupancy dynamics in fragmented landscapes. **Trends in Ecology and Evolution**, Vol. 9, 131-135.

Hanski, I., (1999), **Metapopulation Ecology**. Oxford University Press, Oxford, England.

Hanski, I., Simberloff, D., (1997), The metapopulation approach, its history, conceptual domain and application to conservation. Pp. 5–26 in: Hanski, I., and Gilpin, M., (Eds.), **Metapopulation biology: Ecology, genetics and evolution**. Academic Press, San Diego, USA.

Hanski, I., Ovaskainen, O., (2000), The metapopulation capacity of a fragmented landscape. **Nature**, Vol. 404, 755-758.

Harrison, S., and Bruna, E., (1999), Habitat fragmentation and large-scale conservation: What do we know for sure? **Ecography**, Vol. 22, 225–232.

Heywood, V., (Ed.), (1995), **United Nations environment program: Global biodiversity assessment**. Cambridge University Press, Cambridge, UK.

Hermy, M., Cornelis, J., (2000), Towards a monitoring method and a number of multifaceted and hierarchical biodiversity indicators for urban and suburban parks. **Landscape and Urban Planning**, Vol. 49, 149–162.

Jim, C., Chen, S., (2003), Variations of the treescape in relation to urban development in a Chinese city: The case of Nanjing. **The Professional Geographer**, Vol. 55, 70-82.

Jokimäki, J., (1999), Occurence of breeding bird species in urban parks: Effects of park structure and broadscale variables. **Urban Ecosystems**, Vol. 3, 21–34.

Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., (2003), Spatial similarity of urban bird communities: A multiscale approach. **Journal of Biogeography**, Vol. 30, 1183–1193.

Jongman, R., (1995), Nature conservation planning in Europe: Developing ecological networks. **Landscape and Urban Planning**, Vol. 32, 169–183.

Kates, R., Clark, W., Corell, R., Hall, J., Jaeger, C., Lowe, I., McCarthy, J., Schellnhuber, H., Bolin, B., Dickson, N., Faucheux, S., Gallopin, G., Grübler, A., Huntley, B., Jäger, J., Jodha, N., Kasperson, R., Mabogunje, A., Matson, P., Mooney, H., Moore **III**, B., O'Riordan, T., and Svedin, U. (2001), **Sustainability Science. Science**, Vol. 292, 641 – 642.

Kolar, C., Lodge, D., (2001), Progress in invasion biology: Predicting invaders. **Trends in Ecology and Evolution**, Vol. 16, 199–204.

Kurta, A., Teramino, J., (1992), Bat community structure in an urban park. **Ecography**, Vol. 15, 257–261.

Lautenschlager, R., (1997), Biodiversity is dead. **Wildlife Society Bulletin**, Vol. 25, 679-685.

Levin, S., (1999), **Fragile Dominion**. Perseus Books, Reading, MA, USA.

Levins, R., (1969), Some demographic and genetic consequences of environmental heterogeneity for biological control. **Bulletin of the Entomological Society of America**, Vol. 15, 237-240.

Linehan, J., Gross, M., Finn, J., (1995), Greenway planning: Developing a landscape ecological network approach. **Landscape and Urban Planning**, Vol. 33, 179-193.

Loehle, C., Li, B. (1996), Habitat destruction and the extinction debt revisited. **Ecological Applications**, Vol. 6, 784–789.

Lonsdale, W., (1999), Global patterns of plant invasions and the concept of invasibility. **Ecology**, Vol. 80, 1522–1536.

Luck, M., Jenerette, D., Wu, J., Grimm, N., (2001), The urban funnel model and the spatially heterogeneous ecological footprint. **Ecosystems**, Vol. 4, 782-796.

Luken, R., (2006), Where is developing country industry in sustainable development planning? **International Journal of Sustainable Development**, Vol. 14,1-46.

MacArthur, R., Wilson, E., (1967), **The theory of island biogeography**. Princeton University Press, Princeton, New Jersey, USA.

Maestas, J., Knight, R., Gilgert, W., (2003), Biodiversity across a rural land-use gradient. **Conservation Biology**, Vol. 17, 1425-1434.

Marzluff, J., (2001), Worldwide urbanization and its effects on birds. Pp. 19–47 in: Marzluff, J., Bowman, R., and Donnelly, R., (Eds.), **Avian ecology in an urbanizing world**. Kluwer, Boston, MA, USA.

Marzluff, J., Bowman, R., Donnelly, R., (Eds.), (2001), *Avian ecology in an urbanizing world*. Kluwer, Boston, MA, USA.

McDonnell, M., Pickett, S., (1990), The study of ecosystem structure and function along gradients of urbanization: An unexploited opportunity for ecology. **Ecology**, Vol. 71, 1232–1237.

McGuinness, K., (1984), Equations and explanations in the study of species-area curves. **Biological Reviews of the Cambridge Philosophical Society**, Vol. 59, 423-440.

McIntyre, N., Rango J., Fagan W., Faeth S., (2001), Ground arthropod community structure in a heterogeneous urban environment. **Landscape and Urban Planning**, Vol. 52, 257–274.

McKee, J., Sciulli, P., Fooce, C., Waite, T., (2003), Forecasting global biodiversity threats associated with human population growth. **Biological Conservation**, Vol. 115, 161–164.

McKinney, M., (2006), Urbanization as a major cause of biotic homogenization. **Biological Conservation**, Vol. 127, 247-260.

McKinney, M., Lockwood, J., (1999), Biotic Homogenization: A few winners replacing many losers in the next mass extinction. **Trends in Ecology and Evolution**, Vol. 14, 450–453.

Medley, K., McDonnell, M., Pickett, S., (1995), Forest-landscape structure along an urban-to-rural gradient. **The Professional Geographer**, Vol. 47, 159-168.

Melles, S., Glenn, S., Martin, K., (2003), Urban bird diversity and landscape complexity: Species–environment associations along a multiscale habitat gradient. **Conservation Ecology**, Vol. 7, [online]
URL: http://www.consecol.org/vol7/iss1/art5/

Mittermeier, R., Robles-Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C., Lamoreux, J., Fonseca, G., (2004), **Hotspots**

Revisited: Earth's Biologically Richest and Most Endangered Ecoregions. CEMEX, Mexico City, Mexico.

Morneau, F., DeAcarie, R., Pelletier, R., Lambert, D., DesGranges, J.-L., Savard, J.-P., (1999), Changes in bird abundance and diversity in Montreal Parks over a period of 15 years. **Landscape and Urban Planning**, Vol. 44, 111-121.

Mörtberg, U., Wallentinus, H.-G., (2000), Red-listed forest bird species in an urban environment: Assessment of green space corridors. **Landscape and Urban Planning**, Vol. 50, 215–226.

Murphy, D., (1988), Challenges to biological diversity in urban areas. Pp. 71–76 in: Wilson, E., Peter, F., (Eds.), **Biodiversity**. National Academy Press, Washington, DC, USA.

Myers, N., (1988), Threatened biotas: Hotspots in tropical forests. **Environmentalist**, Vol. 8, 178-208.

Myers, N., Mittermeier, R., Mittermeier, C., Fonseca, G., Kent, J., (2000), Biodiversity hotspots for conservation priorities. **Nature**, Vol. 403, 853–858.

Natuhara, Y., Imai, C., Takeda, H., (1994), Classification and ordination of communities of soil arthropods in an urban park of Osaka City. **Ecological Research**, Vol. 9, 131–141.

Niemelä, J., (1999a), Ecology and urban planning. **Biodiversity Conservation**, Vol. 8, 119-31.

Niemelä, J., (1999b), Is there a need for a theory of urban ecology? **Urban Ecosystems**, Vol. 3, 57–65.

Nilon, C., VanDruff, L., (1987), Analysis of small mammal community data and applications to management of urban greenscapes. **Proceedings of the National Symposium on Urban Wildlife**, Vol. 2, 53–59.

Noss, R., (1992), Indicators for monitoring biodiversity: A hierarchical approach. **Conservation Biology**, Vol. 4, 355–364.

Olff, H., Ritchie, M., (2002), Fragmented nature: Consequences for biodiversity. **Landscape and Urban Planning**, Vol. 58, 83–92.

Olden, J., LeRoy Poff N., McKinney, M., (2006), Forecasting faunal and floral homogenization associated with human population geography in North America. **Biological Conservation**, Vol. 127, 261-271.

Opdam, P., (1991), Metapopulation theory and habitat protection: A review of holarctic breeding bird studies. **Landscape Ecology**, Vol. 5, 93-106.

Opdam, P., Steingröver, E., van Rooij, S., (2006), Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. **Landscape and Urban Planning**, Vol. 75, 322–332.

Park, C.-R., Lee, W.-S., (2000), Relationship between species composition and area in breeding birds of urban woods in Seoul, Korea. **Landscape and Urban Planning**, Vol. 51, 29–36.

Parris, K., (2006), Urban amphibian assemblages as metacommunities. **Journal of Animal Ecology**, Vol. 75, 757-764.

Pezzoli, K., (2000), **Human Settlements and Planning for Ecological Sustainability**. MIT Press, London, England.

Pickett, A., Cadenasso, M., (2006), Advancing urban ecological studies: Frameworks, concepts, and results from the Baltimore ecosystem study. **Austral Ecology**, Vol. 31, 114-125.

Pimentel, D., Lach, L., Zuniga, R., Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. **BioScience** Vol. 50,53-65.

Porter, E., Forschner, B., Blair, R., (2001), Woody vegetation and canopy fragmentation along a forest-to-urban gradient. **Urban Ecosystems**, Vol. 5, 131–151.

Pulliam, H., (1988), Sources, sinks, and population regulation. **American Naturalist**, Vol. 132, 652-661.

Pysek, P., (1993), Factors affecting the diversity of flora and vegetation in central European settlements. **Vegetation**, Vol. 106, 89–100.

Pysek, P., (1998), Alien and native species in Central European urban floras: A quantitative comparison. **Journal of Biogeography**, Vol. 25, 155–163.

Quammen, D., (1996), **Song of the dodo**. Simon and Schuster, New York, USA.

Rebele, F., (1994), Urban ecology and special features of urban ecosystems. **Global Ecology and Biogeography Letters**, Vol. 4, 173-187.

Rubbo, M., Kiesecker, J., (2005), Amphibian breeding distribution in an urbanized landscape. **Conservation Biology**, Vol. 19, 504-511.

Sandström, U., (2002), Green infrastructure planning in Sweden. **Planning, Practice and Research**, Vol. 17, 373-385.

Sandström, U., Angelstam, P., Khakee, A., (2006a), Urban comprehensive planning: Identifying barriers for the maintenance of functional habitat networks. **Landscape and Urban Planning**, Vol. 75, 43–57.

Sandström, U., Angelstam, P., Mikusinski, G., (2006b), Ecological diversity of birds in relation to the structure of urban green space. **Landscape and Urban Planning**, Vol. 77, 39-53.

Savard, J.-P., Clergeau, P., Mennechez, G., (2000), Biodiversity concepts and urban ecosystems. **Landscape and Urban Planning**, Vol. 48, 131-142.

Scott, J., Heglund, P., Morrison, M., Haufler, J., Raphael, M., Samson, F., (Eds.), (2002), **Predicting species occurrences: Issues of scale and accuracy**. Island Press, Covello, CA, USA.

Sekerciolu, C., Daily, G., Ehrlich, P., (2004), Ecosystem consequences of bird declines. **Proceedings of the National Academy of Science**, Vol. 101, 18042-18047.

Shaffer, M., (1981), Minimum population sizes for species conservation. **BioScience**, Vol. 31, 131–134.

Shea, K., Chesson, P., (2002), Community ecology theory can be used to understand biological invasions. **TRENDS in Ecology & Evolution**, Vol. 17, 170-176.

Simberloff, D., (1988), The contribution of population and community biology to conservation science. **Annual Review of Ecology and Systematics**, Vol. 19, 473-511.

Slocombe, D., (1993), Environmental planning, ecosystem science, and ecosystem approaches for integrating environment and development. **Environmental Management**, Vol. 17, 1432-1439.

Small, E., Sadler, J., Fiszpan, H., Tefler, M., (2006), Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. **Journal of Biogeography**, Vol. 33, 1126-1138.

Soulé, M., (1985), What is conservation biology? **Bioscience,** Vol. 35, 727-734.

Standley, L., (2003), Flora of Needham, Massachusetts – 100 years of floristic change. **Rhodora**, Vol. 105, 354–378.

Tait, C., Daniels, C., Hill, R., (2005), Changes in species assemblages within the Adelaide Metropolitan Area, Australia, 1836–2002. **Ecological Applications**, Vol. 15, 346-359.

Taylor, A., (1990), Metapopulations, dispersal and predator-prey dynamics: An overview. **Ecology**, Vol. 71, 429-433.

Tilman, D., May, R., Lehman, C., Nowak, M., (1994), Habitat destruction and the extinction debt. **Nature**, Vol. 371, 65-66.

Tjorve, E., (2003), Shapes and functions of species-area curves: A review of possible models. **Journal of Biogeography**, Vol. 30, 827-835.

UNCED, (1992), **Convention on biological diversity**. Department of Public Information, United Nations, New York, USA.

UNCHS, (1996), **An urbanizing world: Global report on human settlements**. Oxford University Press, New York, USA.

UNEP, (1995), **Global biodiversity assessment: Summary for policy-makers**. Cambridge University Press, Cambridge, UK.

UNPD, (2006), **World urbanization prospects: The 2005 revision**. [http://esa.un.org/unup/p2k0data.asp]

Van der Veken, S., Verheyen, K., Hermy, M., (2004), Plant species loss in an urban area (Turnhout, Belgium) from 1880 to 1999 and its environmental determinants. **Flora**, Vol. 199, 516-523.

Vitousek, P., (1990), Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. **Oikos**, Vol. 57, 7–13.

Vitousek, P., Mooney, H., Lubchenco, J., Melillo, J., (1997), Human domination of Earth's ecosystems. **Science**, Vol. 277, 494–499.

Wackernagel, M. Rees, W., (1996), **Our ecological footprint: Reducing human impact on the earth**. The New Catalyst Bioregional Series, New Society Publishers, Vancouver, Canada.

Wakermagel, M., Schulz, N., Dumling, D., Linares, A., Jenkins, M., Kapos, V., Monfreda, C., Loh, J., Myers, N., Norgaard, R., Randers, J., (2002), Tracing the ecological overshoot of the human economy. **Proceedings of the National Academy of Science,** Vol. 99, 9266–9271.

Walker, B., (1992), Biodiversity and ecological redundancy. **Conservation Biology**, Vol. 6, 18–23.

Walmsley, A., (1995), Greenways and the making of urban form. **Landscape and Urban Planning**, Vol. 33, 81–127.

Wang, Y., Moskovitz, D., (2001), Tracking fragmentation of natural communities and changes in land cover: Applications of landsat data for conservation in an urban landscape (Chicago Wilderness). **Conservation Biology**, Vol. 15, 835-842.

WCED, (1987), **Our Common Future**. Oxford University Press, New York, USA.

Weifeng, L., Zhiyun, O., Xuesong, M. Xiaoke, W., (2006), Plant species composition in relation to green cover configuration and function of urban parks in Beijing, China. **Ecological Research**, Vol. 21, 1440-1703

West, N., (1993), Biodiversity of rangelands. **Journal of Range Management**, Vol. 46, 2-13.

Wilcox, B. Murphy, D., (1995), Conservation strategy: The effects of fragmentation on extinction. *American Naturalist*, Vol. 125, 879-887.

Williams, N., Morgam, J., McDonnell, M., McCarthy, M., (2005), Plant traits and local extinctions in natural grasslands along an urban–rural gradient. **Journal of Ecology**, Vol. 93, 1203-1213.

Wilson, E., Willis, E., (1975), Applied biogeography. Pp. 523–534 in: Cody, M., and Diamond, J. (Eds.), **Ecology and Evolution of Communities**. Harvard University Press, Cambridge, USA.

Wood, B., Pullin, A., (2002), Persistence of species in a fragmented urban landscape: The importance of dispersal ability and habitat availability for grassland butterflies. **Biodiversity and Conservation**, Vol. 11, 1451–1468.

Woodward, J., Eyre, M., Luff, M., (2003), Beetles (Coleoptera) on brownfield sites in England: An important conservation resource? **Journal of Insect Conservation**, Vol. 7, 223–231.

WRI, (1997), **World resources: 1996-1997**. World Resources Institute, Washington, DC, USA.

Wu, J., Loucks, O., (1995), From balance of nature to hierarchial patch dynamics: A paradigm shift in ecology. **Quarterly Review of Biology**, Vol. 70, 439-466.

Yokohari, M., Takeuchi, K., Watanabe, T., Yokota, S., (2000), Beyond greenbelts and zoning: A new planning concept for the environment of Asian mega-cities. **Landscape and Urban Planning**, Vol. 47, 159–171.

Zerbe, S., Maurer, U., Schmitz, S., Sukopp, H. (2003), Biodiversity in Berlin and its potential for nature conservation. **Landscape and Urban Planning**, Vol. 62, 139–148