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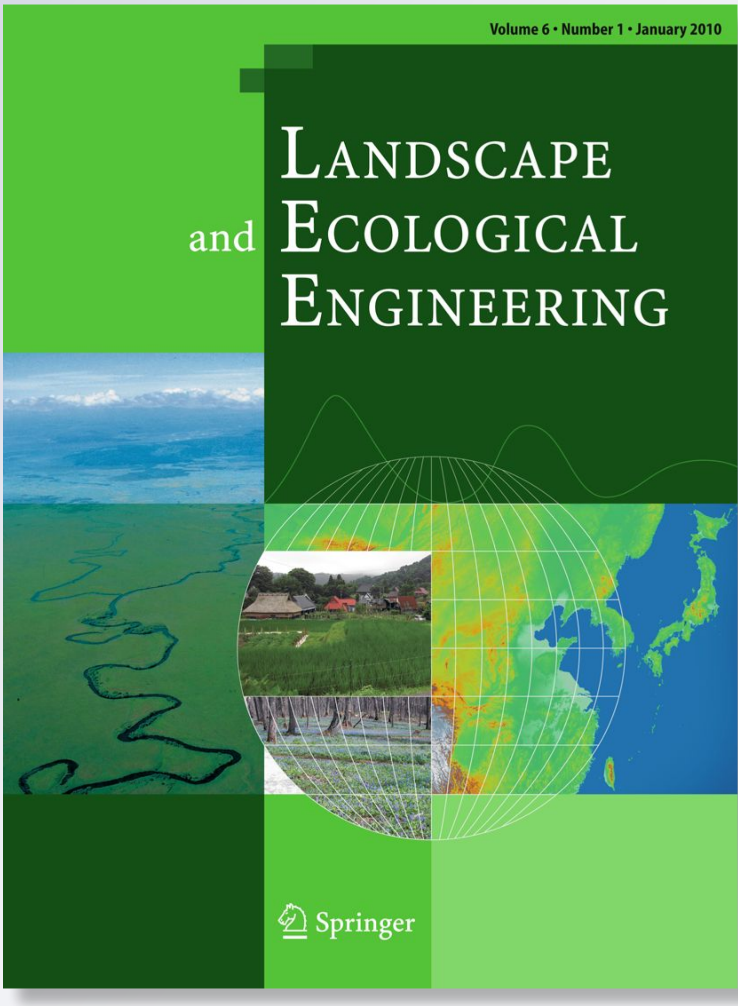

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Biodiversity and Ecosystem Services: Importance of Cities for post 2010 perspective

The ecology of urban areas and their functions for species diversity

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Abstract Despite the appearance of an enormous number of publications about urban ecology and species diversity, many issues are simply opened up rather than explained. The ecological complexity of urban areas, i.e., the variety of determinants and the spatial and temporal dynamic of cities, preclude simple starting points and lines of explanation. Therefore, we lack sufficient comparisons between various cities, especially comparisons on a global level. If cities are to be compared by appropriate indicators, and if they are to be evaluated with respect to urban biodiversity, then models are necessary that help us understand and mirror the causal relationships between urban areas and biological diversity. Three approaches, also representing a multiscaled view of urban areas, are presented that are suitable for developing applicable models and indicators for monitoring ecological systems: the embedded city, the urban matrix, and urban patches. The embedded city represents a globally useful concept, because the relationship between cities and their regions can be applied as an indicator to all regions. The lack of sufficient description of the urban matrix makes comparisons between cities difficult and causes scientists to underestimate the importance and function of the matrix for urban biodiversity. Urban patches are often investigated in urban studies about plants and animals. Therefore, much existing data can be used, and several criteria describing the functions of patches for biodiversity are available. In particular, the first two approaches should be researched more intensively.

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Introduction

Although the relationship between the urban environment and the occurrence of plants and animals is well known, both in general (e.g., the characteristics of urban flora and fauna with respect to the urban heat island) and in detail for some cities and towns, [e.g., comprehensive surveys of Berlin (Sukopp 1990), Chiba (Numata 1979–1982), and New York (Kieran 1959)] or for specific urban habitats (e.g., city parks, railways, cemeteries), great problems exist in understanding the variety of species diversity in different cities (Werner and Zahner 2009). A city is defined by several fundamental characteristics that universal around the planet and that influence both the ecology and the biological diversity of urban areas. Attributes of major cities are:

- a high population density;
- a conglomerate arrangement of buildings, technical infrastructure, and open space—the urban mosaic;
- the development of a separate climate;
- an alteration of the hydrological balance;
- both selective and diffuse input of nutrient sources;
- a multitude of landscaped green areas and gardens that include diverse and highly productive vegetation;
- various man-made bodies of water;
- intentional or unintentional increase in animal food sources;
- pollutants in air, water, and soil;
- various disturbance and stress factors, such as soil compaction, nuisance noise, and light pollution;

- numerous small-scale open and green spaces including seminatural areas;
- frequent intentional or unintentional introduction of alien animal and plant species;
- high percentage of so-called generalists and common species.

(McDonnell et al. 1997; Pickett et al. 1997, 2006; Sukopp and Wittig 1998; Grimm et al. 2000; Alberti 2008; Forys and Allen 2005; Shochat et al. 2006) McDonnell and Hahs (2008) argue that a set of variables should be used to make comparisons possible between various cities, and Andersson et al. (2009) concluded that multivariate views and analyses are needed to compare cities and investigate how urbanization influences the ecological character in different parts of a city.

In the general discussion about biodiversity, it is emphasized that understanding the mechanisms with respect to interactions between local and regional patterns of species distribution remains challenging and that studies of interactive effects of multiple mechanisms at multiple scales are needed (Collins et al. 2002), and that is especially true for cities. The spatial heterogeneity and the dynamic of the urban landscape are the result of complex interactions of abiotic and biotic processes at different scales, precluding simple starting points and lines of explanations (Schröder and Seppelt 2006). On the other hand, our knowledge is not really unbiased. There are three examples for this: (1) We have a limited view due to the fact that an overwhelming number of published studies present results from regions in central Europe and North America. (2) Our common scientific knowledge and perception of biological diversity in cities are particularly determined by two taxonomic groups—higher plants and birds; roughly estimated, more than two thirds of all published studies deal with these two groups (Sukopp et al. 1986–2000). (3) Comparing the floristic maps of European cities, one notices the cities exhibiting a higher diversity of species are those within which bounds reside universities and their associated biologists.

Therefore, we lack sufficient comparisons between various cities, especially comparisons on a global level. To understand species diversity of cities in general and to assess species diversity of a single city in relation to other cities, analyses have to cover various scales (Whittaker et al. 2001). In this article, I demonstrate three approaches toward a better understanding of the relationship between patterns and processes of cities and species diversity. Coincidentally, the three approaches represent three scales—from local to regional—following the hierarchy theory in ecology, that the system (in this case, the city) that is in the focus of interest has also to be a subject of up- and downscaling procedures (Wu et al. 2006). The approaches are: the embedded city, the urban matrix, and urban patches.

The embedded city

Plant and animal species living in cities are part of the regional pool of species. Urban areas contribute to changes but also to conservation and protection of this regional pool of species. A primary goal in protection and planning is the conservation of native species. Based on the main goal mentioned above, namely, to conserve and support indigenous plants and animals in regions under urban influence (McKinney 2006), the aspired aim must be to develop cities in such a fashion as to be better integrated into their natural biogeographic surroundings. Hereby, the cornerstone of sustainable development is defined as maintaining a balance with the natural landscape. However, in my opinion, this is not to lead to the idea of cities dissolving into their resident natural landscapes. Cities will remain independent landscapes and habitats that maintain a unique ecological character in respect to biological diversity. The main urban features mentioned in the “Introduction” will not disappear as long as urban areas maintain their functions for humans.

To obtain a general understanding of the relation between urban areas and the surrounding region, it seems necessary to point out two aspects. First, an ecological description of a city in comparison with its environ is required that is more globally interpreted than generally custom. To master that point, that would allow achievement of better comparisons between results of local investigations from different cities. Second, the regional pool of species must be understood as an extensive as well as a dynamic pool of species. This means the regional pool should not be reduced to limited cross-sections of species living in natural or seminatural habitats and to an unchanging configuration of species.

Embedded in space

To the first aspect: if the ecology and biological diversity of urban areas is described, it is often compared with the ecology and diversity of the surrounding areas. Many studies reveal that urban areas are warmer or dryer and that forest habitats within urban areas are more fragmented than forests outside of them (Gilbert 1989; White et al. 2002; Mabelis 2005). As mentioned earlier, these statements are based on investigations conducted mostly in the northern hemisphere, where birds and forested areas are mainly used as the species and habitats of reference (Vallet et al. 2008). This is true especially in regard to studies on the effects of fragmentation processes. However, towns and cities are embedded in varying biogeographical regions and landscape settings. Subsequently, a global viewpoint is necessary to obtain a general understanding of the interrelations of cities and their surroundings. These basic traits of urban areas encounter many different natural existing conditions and landscapes of the different biomes that have been more or less substantially modified by human influence (Palmer et al. 2008). Therefore, cities embedded in the three different biospheres—boreal forests, deserts, and savannahs—are presented as examples.

The vegetation zone of boreal forests is characterized by extensive coniferous woodland, shady lighting conditions, a relative shortage of nutrients in the soil, moderate temperatures in summer, and an extended winter. Only few disturbance-tolerant species occur in these woodlands. Taking into account the description of urban areas above, cities constitute a considerable contrast to these woodlands, especially in winter. Cities such as, for instance, Oslo (Norway) or Vancouver (Canada) are remarkably warmer than surrounding environs, and the growing season is noticably longer. Urban open spaces represent mostly open, productive landscapes replete with disturbance. Because of the distinct seasonality of summer and winter, urban areas have a special function in winter and serve as shelter for many species (Clergeau et al. 1998; Murgui 2009). Species whose natural distribution areas lie further south can selectively move the borders of their native environment further north (Luniak 2004; Kowarik and Säumel 2007).

The hot and dry deserts located in several parts of the world differ largely by their floral composition, but the basic attributes of all deserts are the scarce growth of vegetation and the low (diminished) fertility of the soil due to water scarcity. Because of these extreme temperature and water conditions, the composition of the regional flora and fauna is dominated by specialists adapted to these harsh circumstances. The vegetation consists of dwarf bushes and trees, and many indigenous animal species are bound to small habitats with limited space. The variation between dry and humid years greatly influences vegetation development (Buyantuyeva et al. 2010). Cities of these extremely arid zones, such as, for instance, Dubai (United Arab Emirates) or Phoenix (United States) are not dryer but are more humid than the surrounding natural areas due to the presence of numerous artificial bodies of water and the irrigation of parks, house gardens, or even streets (Pickett and Cadenasso 2009). Additional irrigation also causes an adjustment, but not a complete parity, between dry and humid years. Thus, there are more green areas, woody elements are increased in size, and the generalists among animals find sufficient habitats.

Savannahs, respectively tropical and subtropical grasslands are, as is implicated by the name, characterized by grassy plants. The landscape exhibits isolated scattered trees. The climate in these areas shows severe changes from rainy periods to relatively long periods of drought, which can last for more than 6 months in some regions. The soils vary in fertility. Large grazers keep the percentage of woody elements low, and periodical burnings favor species adapted to strong disturbances and disastrous events. Urban parks also feature large grassy spaces and single trees or bushes or islands of woody elements planted in a scattered manner. Plants and animals of the savannah acclimated to disturbances will find adequate habitats in the cities. It is to be expected that cities located in the biomes of the savannah, such as, for instance, Pretoria (South Africa) or Brasilia (Brasil), provide suitable habitats for several species occurring in the surrounding areas, but there is a lack of investigations to check that point. Animal species dependent on extensive open planes, as open space in cities is parcelled, or plants dependant on competition advantages and seed dispersal by grazing animals have a great risk of extinction in urban landscapes (Williams et al. 2005). The seasonality between rainy and dry season is identifiable in cities, too. In cities, the number of species fluctuates considerably between wet and dry seasons (Torga et al. 2007).

According to the aforementioned proposed notions, one would expect the urban areas of a savannah to reflect a higher percentage of native flora and fauna than cities located in biomes of the deserts and boreal forests. Unfortunately, no study has been conducted to systematically analyze this aspect. But as examples of Australian cities drastically demonstrate, further factors, such as the length of time since the cultural reshaping of the original (pristine) landscape and the time lapse since urban development processes also play an important role (Tait et al. 2005). I agree with Hahs et al. (2009) that the geography of cities is confounded with the history of cities, and that is a source of uncertainty.

Embedded in processes of time and exchange

Cities and their environments are not static over time. Many European cities were founded several hundred years ago. In contrast to many Asian and South American cities, they grew more gradually and continue to do so to this day. They are also of a more limited scale, and the above holds true for their surrounding areas as well. More than 10,000 years ago, humans began engaging in land cultivation in different parts of the world and thereby changed the pristine, natural landscape into a cultural landscape (Boyden 1979). With the small-scaled rural landscape, the process of human-made fragmentation started and became a main factor influencing the landscape (Pearson et al. 2004). Thus, the natural regional pool of species was supplemented by new species, because new species were introduced or emerged by the human impact. On the regional scale, interaction began between species occurring in cultivated and natural habitats. A new species pool sprang up in the region, and of this new pool of species, the ones most adapted to human disturbance and fragmentation were selected.

Ancient urban civilizations evolved from existing cultural landscapes about 5,000 years ago. The third mode of land utilization—urban settlements—was introduced, forming the regional pool of species on a small scale at first. Today, large areas of the globe are influenced and formed by extended urban agglomerations. With continuing expansion of trade relations, the regional pool of species was further supplemented by species of other biogeographical regions.

The time period—the time of coevolution—in which the regional pool of species is formed under the influence of silvicultural and agricultural, as well as urban, development determines the relationship of regional versus urban species pools. Over the course of the last 3,000 years, landscapes created by humans were to be found in Europe, particularly in Mediterranean regions. Both the rural and the urban landscape are based on long adaptation processes to anthropogenic influence. A relatively great similarity exists between the Mediterranean landscape and green structures in cities, not only because both consist of open, sparsely forested land but also because the land was (and in part still is) parcelled. The city of Rome (Italy) is a good example of this. Compared with cities of central Europe, Rome exhibits a relatively high percentage of indigenous vascular plants of the region (Celesti-Grapow et al. 2006). In contrast, this proximity to cultivated land may not be a given in certain ecological systems that create unusual habitats, such as, for instance, rice paddies. Paddies have also been cultivated in Japan for 2,000–3,000 years (Natuhara 2007). Nonetheless, only few habitats in cities, such as ponds or seas in parks, exist in close proximity to paddies. Therefore, only a few interrelations can be observed.

In central Europe of the twelfth and thirteenth centuries, when the first high phase of urban development started, the interplay of natural, cultivated, and urban landscape took place, lasting for nearly 1,000 years. The interaction between natural landscape and land cultivated by humans goes back even further (Ellenberg 1982). In North America, however, it has not even been 500 years since humans transformed large areas of natural landscapes into cultivated land. Similarly in Australia and New Zealand, only 200 years have passed since systematic (formation of settlements) colonization took place. On both continents, a large number of plants and animals already accustomed to cultivated and urban landscapes was introduced by early settlement (Müller et al. 2010). Consequently, these species were present from the onset of anthropogenic change. In addition, a highly isolated indigenous fauna and flora existed in Australia and New Zealand that reacted especially sensitively to changes caused by colonization. Therefore, settlements in those countries show a much greater ecological distance to the surrounding bioregion, and the effects caused by urban activities were more severe than in Europe. The significance of the time lapse since the beginning of anthropological (cultural, urbanizational) influence can be demonstrated best by exploring the relationship of indigenous to alien species; Table 1 shows that correlation by some selected examples. Here, indigenous or native species are defined as species that have originated in a given area with or without human involvement or that arrived there from an area in which they are native without intentional or unintentional human intervention (Scholz 2007). Alien or nonnative species are those that arrive in a given area with intentional or unintentional human involvement (Scholz 2007), including species native to other areas of the country/continent but formerly foreign to the defined region (Tait et al. 2005).

The source populations of migratory species, in particular, are often found in the surroundings of cities and not in the cities themselves. Continuous migration of individuals from the environs into the cities contributes to the stability of urban populations (Schwarz and Flade 2000). These movements also enhance the genetic exchange between

Table 1 Proportion of native species with respect to cities of different regional and local histories

City	Area (km^2)	Number of plant species	Percent native species (incl. archaeophytes)	Authors
Rome (Italy)	1,272 300 (city)	1,293	88	Celesti-Grapow et al. (2006)
Chonju (South Korea)	206	525	83	Zerbe et al. (2004)
Berlin (Germany)	892	1,393	80	Prasse et al. (2001)
New York (USA)	1,214 789 (terrestrial)	2,177	62	DeCandido et al. (2004)
Christchurch (New Zealand)	1,426 452 (city)	317	15	Ignatieva et al. (2000)

populations within and outside of urban areas. Consequently, changes in the surrounding environs—such as, for instance, massive industrial reorganization—can actually endanger urban populations regardless of the quality of the habitats in the cities (Tait et al. 2005). This emphasizes the importance of considering the interrelation between urban areas and the surrounding landscapes. Contrarily, cities often serve as a source of exotic species spreading into the environs. It should be mentioned that studies conducted on birds and vascular plants in North America and Australia show that the dominance of alien species arose only after a certain period of time (Clemants and Moore 2003; Tait et al. 2005). In the region of Adelaide, most native bird species became extinct only in the last 30 years. This may be linked to the generation period of these species or to major changes in periurban landscapes (Tait et al. 2005). In the central European environment, urban growth tends to take place primarily on agricultural land. Whereas this also occurs in areas with rapid suburbanization (such as in the United States) or rapidly growing megacities, these scenarios are also likely to have a direct impact on areas of near-natural wilderness (Grove et al. 2005). This results in very different interactions at the urban periphery.

The ecological distance between urban species composition and that of the surrounding areas serves as a useful indicator of urbanization's impact on biodiversity. Therefore, a measure of this distance is appropriate for comparative indices. However, to evaluate various cities with respect to biodiversity, the spatial, temporal, and historical contexts, as mentioned above, must be considered. In order to generate specific distance indices, reference parameters—biogeographical region and regional pool of species—must be defined. As a prerequisite in developing the aforementioned distance indices, one must ensure that the scale of the habitat as well as species richness may be delimited to objective and reproducible units. As large-scale studies often operate in terms of grids, these ought to be juxtaposed on natural boundaries. For the time being, the term "regional pool of species" should be defined objectively. This is to suggest that all species are to be included, irrespective of their origin. In other words, included are all species that have become a permanent element of the regional wild flora and fauna, regardless of whether found in natural, cultivated, or urban landscapes. In subsequent steps, only indicators allowing differentiations and implicating values (e.g., proportion of species of the Red Data Lists) should be applied. Shifts in the relation between native and alien species or between functional groups that take place in an observed city with respect to regional species composition are adequate indicators to demonstrate how well this city is integrated into the biogeographical region. This information can be used for targets and measures in planning processes.

In order to make universal comparisons, additional parameters are required (as mentioned above), or the classification of different categories must be made. There are distinct differences in the value of these indicators depending on the natural landscape (boreal coniferous forest versus desert) or the time since cultivation (Mediterranean vs. New Zealand). Urban areas mostly evolved in geographical regions that are naturally rich in species (Kühn et al. 2004). So there is a special responsibility and need to implement conservational measures. For example, the Satoyama principle is a concept that describes appropriate measures for conserving and securing biodiversity in landscapes under anthropological influence (Takeuchi et al. 2002).

The urban matrix

The significance of the so-called urban matrix for biodiversity in cities is underestimated. Habitat patches are defined from a human perspective, and the matrix is considered nonhabitat (Franklin and Lindenmayer 2009), but there are two important functions of the matrix: (1) presenting a habitat for flora and fauna, and (2) presenting possibilities for plants and animals to move through urban areas. The permeability of the urban matrix (in the strict sense of the word) is characterized strongly by the amount of greenery and other barrier effects and influences flora and fauna movement. Enhancement of these two functions of the matrix (living space and permeability for animals and plants) should constitute the goal for future planning.

What is the urban matrix?

Structurally, a town or city can be viewed as a complex habitat mosaic (Mazerolle and Villard 1999). This habitat mosaic is made up of varying subunits. The matrix, the dominant component in the landscape, is the most extensive and connected landscape type, and it plays the dominant role in landscape functioning. With respect to a city, the built-up areas represent a mix of buildings, streets, and open space; small areas of green are the dominant landscape elements and are the glue that binds a city (Forman and Godron 1986). The urban matrix is not homogenous. It is composed of areas of high- and low-density building clusters and parts with a high or low level of disturbance. In addition, there are breaks in the matrix caused by large green areas or linear structures such as rivers, motorways, and railway tracks. That means cities differ in the following aspects: how compactly they are organized; how interspersed they are with greenery; how many islands of high building density are present; what the ancillary barrier effects are. The various mix by both scales, the alternation between built-up and open areas, and the mix of buildings and vegetation on the built-up areas, give each city its own, unique habitat mosaic.

The respectively unique habitat mosaic is in turn linked to the specific quality of species richness and distribution. This should be the case in theory, even if large areas of flora and fauna are identical in different cities of the same biogeographical region. If these habitat mosaics of different cities could be illustrated by defined, basic models of the spatial organization of cities, then these models could be compared regarding their effects on biological diversity. However, those basic models are difficult to describe because of the multidimensionality and high variability across space (Godefroid and Koedam 2007). Indicators are necessary to adequately describe and evaluate the spatial structure of a city as a whole in respect to biological diversity. In my opinion, no concrete perspectives on suitable measures and indicators exist to properly compare urban areas to one another. However, broader and simpler definitions do exist for the term urban matrix. These definitions simply state that everything outside patches is considered matrix. In other interpretations, all urban green spaces are considered matrix, as remaining near-natural areas in a city are defined as patches (Er et al. 2005; Palmer et al. 2008). Normally, the term urban matrix is not precisely defined. It becomes clear that the description of the matrix depends largely on the vantage point. What is seen and mapped as a patch (for example, 0.5 or 5 ha) or as a boundary (interruption break) in the matrix (for example, small streams or only big rivers) depends on the scale.

Underestimation of the urban matrix

Relatively few studies have investigated correlations between the layout of the urban matrix and biological diversity (Hodgkison 2005). One reason the urban matrix has not been researched in regard to biodiversity in the city is simply the fact that the matrix consists mainly of private property that cannot be accessed and studied as easily as public open space (Hodgson et al. 2007). There is increasing evidence that application of the urban matrix in terms of biological diversity in cities has been underestimated until now (Crooks 2002; Hodgson et al. 2007; Loeb et al. 2009).

In the following, some examples are presented emphasizing the importance of the urban matrix for biological diversity in urban areas. The results of recent studies reveal a high penetration of birds (Hodgson et al. 2007), bats (Loeb et al. 2009), and small mammals (Crooks 2002) into well-greened built-up areas. If a park is surrounded by such green built-up areas, the space for habitat is increased. Small parks may therefore provide qualities of shelter and living space for animals similar to those of a larger park that is isolated by barriers from the surrounding space (Loeb et al. 2009). Study of the red squirrel showed that explanatory models of its incidence in patches are significantly better if the permeability of the matrix is taken into account in the analysis (Verbeylen et al. 2003). It is estimated that in the United Kingdom, for example, between 19% and 27% of the area of towns and cities is taken up by domestic gardens (Smith et al. 2006), providing high-quality habitats for plants and animals. As demonstrated on wood mice, the domestic gardens may further reduce the deleterious effects of fragmentation (Baker et al. 2003). Many residential districts in central Europe have a green index—the portion of the surface covered by vegetation—of 50% or more and contrasts with other types of land use in having a large number of microhabitats (McIntyre et al. 2001). In medium-sized towns in Germany alone, the combined green areas between multistory buildings (which can definitely show a highly diverse vegetation structure) may be an area larger than that of all public green spaces (Werner 1999). That is a great potential influencing species distribution in urban areas. Improving matrix quality may lead to higher conservation returns than manipulating the size and configuration of remnant patches for many of the species that persist in urban areas (Franklin and Lindenmayer 2009).

Analyzing and indicating the urban matrix

Perspectives to analyze the urban matrix may possibly derive from the following two methodological approaches. The first approach is to segment cities into component parts. The foundation of this method is to divide the city into so-called urban structure types and selectively allot the number of species to the respective structure type. This procedure was developed in Germany in the context of mapping urban biotopes and has been adopted abroad (Schulte et al. 1993). In the United States and Australia, the importance of differentiating urban areas into city structure types for urban ecological studies has now been tested (Cadenasso et al. 2007; Hahs and McDonnell 2006). The second approach is the widely used analysis of the interrelation of urbanization and biological diversity along urban–rural gradients. This method has been applied in numerous studies, as the review of McKinney (2008) demonstrates. Results, however, are only comparable to a certain extent, as reference sections and definitions chosen as parameters of urbanization often vary. In many studies, only patches classified along the urban–rural gradient were analyzed and not the areas between them. An exception was the study by Zerbe et al. (2003), which compared not only various scales but also both patches and urban structures. McDonnell and Hahs (2008) present important suggestions concerning the conduction of well-designed urban–rural gradient analyses.

Resistance and permeability are terms that should be used to describe the urban matrix and to get an understanding of the relationship between urban areas and biodiversity. We have no indicators or sufficient methods to identify those traits of the urban matrix. There is a correlation between the general degree of vegetation cover to and species richness in a city. If the proportion of green areas and vegetation elements is high, then more species can exist in and move across the urban matrix. Therefore, the amount of urban vegetation can be used as an indicator for evaluating the quality of a matrix. Remote sensing can establish the proportion of green areas of a city in satellite pictures. The results can be further improved by investigating vegetation quantitatively and qualitatively (such as the percentage of woody elements etc.).

There is no proper indicator that can be used for comparative evaluation of habitat mosaics as a whole. A very basic indicator for describing characteristics of a city in respect to biological diversity is the species–area curve. Should the values of a given city differ from those of the mean, this may suggest either a surplus or deficit in biodiversity. One gets a first impression of the situation of one's city and can then think about planning needs for maintaining or developing biodiversity. In relation to other cities in central Europe, Berlin shows an exceptionally high number of plant species. Berlin covers approximately 890 km^2 and harbors >1,390 vascular plant species (Table 1). There are suggestions for central Europe to define areas as hot spots of biodiversity if there are >1,300 plant species within 1,000 km^2 (Hobohn 2005). According to that definition, Berlin is a hotspot of biodiversity in Europe. A comparison is only possible provided that the setting of spatial boundaries of urban areas is equivalent and the biogeographical region is comparable. Thus, Cape Town (South Africa), located in one of the global hotspots of biodiversity and exhibiting >9,500 plant species, should not be compared with Berlin (Germany) or Warsaw (Poland) with "only" 1,390 and 1,100 plant species, respectively. For such global comparisons, corresponding classifications or adaptation factors should be created. The species–area curve indicator leaves too many questions unanswered to be reasonably applied.

Additionally, it is helpful to establish systems to distinguish matrix-occupying and matrix-sensitive species. Garden et al. (2006) define matrix-occupying species as species using the matrix and moving more or less freely. By contrast, species for which the built-up areas represent barriers are termed matrix-sensitive species. Cook et al. (2002) and Godefroid and Koedam (2003) established that matrix-occupying species also occupy patches and that, because of this, effects of patch size or distances between patches on species diversity may be concealed. Matrix-sensitive species are exposed to greater risks to local extirpation because of fragmentation and other potential changes to their habitat (Crooks et al. 2004). If matrix-occupying species are omitted from the analysis of patch effects, clearer correlations between the structural characteristics of patches and species diversity can be identified. If flora and fauna undergo a systematical classification into these two categories, then a breakdown of proportions may be an effective supplemental indicator. However, it is to be expected that this classification of individual species will vary from region to region.

Urban patches

Remnants of natural and seminatural landscapes, parks, green spaces, wastelands, and other vegetation areas constitute the green skeleton, the green infrastructure that contributes to the biological diversity of a city. The conservation and development of this green infrastructure is an important challenge of urban planning. In this regard, the quality of individual patches and quality of the system as a whole must be considered. No model exists describing the correlation between quality of the system of green infrastructure and biodiversity of cities. However, there is a multitude of indicators to specify individual aspects (e.g., size of an area, distribution and size of structural elements, and degree of connectivity) and especially to classify and evaluate the quality of individual habitat, because they are indicators used in nature conservation strategies and planning concepts in general.

A large number of investigations and published studies deal with remnants and patches in urban areas with respect to several taxonomic groups and single species that are beyond the scope of this paper. Reviews and comprehensive collections can be found in, for example, Marzluff et al. (2001), Kelcey and Rheinwald (2005), Werner and Zahner (2009), and Müller et al. (2010). Following are a few particular aspects regarding the significance of green infrastructure (limited to individual patches) in regard to biodiversity. The general factors that influence the quality of green space and habitats is demonstrated. The importance of urban parks for regarding the biodiversity of a landscape characterized by urban use is clearly illustrated by a study from Flanders, Belgium. The investigated urban parks of Flanders encompass only about 0.03% of the area but accommodate about 29% of all wild plants and >48% of all breeding birds in the region. In addition, many rare and endangered species are found in urban near-natural remnant areas. These remaining spaces do not only exist in the urban fringe but also in the middle of megacities. Notable examples of pristine remnants, even partly located in the middle of a city, are: in Rio de Janeiro (Brazil), the remnant forests of the Mata Atlantica; in Singapore, the evergreen forests of the Botanical Garden; in Caracas (Venezuela), the National Park El Avila with its rock faces; in the Australian metropolitan areas of the cities of Perth, Sydney, and Brisbane, various remnants of bush land; in York (Canada) and Portland (USA), remnants of natural forests, and in Edinburgh (Scotland), rock faces and outcrops (Heywood 1996; Miller and Hobbs 2002, Edinburgh Biodiversity Partnership, no year).

Various authors report a positive correlation both between native vegetation elements and species richness (Chace and Walsh 2006) and between native vegetation elements and, for example, native bird species or arthropods (McIntyre et al. 2001; Daniels and Kirkpatrick 2006). Turner (2006) reports similar findings for the city of Tucson, USA: the strongest positive correlation with the abundance and diversity of native birds is with the amount of native vegetation, in this case the bushy vegetation of the desert landscape. In a comparison of various domestic gardens, Parsons et al. (2006) conclude that more native birds are to be found in gardens with predominantly native vegetation. Turner et al. (2005) refer to the fact that only a few nonnative species are found at sites with natural and seminatural vegetation. They conclude that near-natural vegetation increases robustness and hence resistance to the intrusion of species foreign to the area.

Following downscaling, urban patches are the microscale, and at that scale, we must deal with the specific ecological conditions of a location. A number of authors state that in terms of biological diversity, the quality of habitats is determined by their soil parameters (especially for plants and soil fauna), structural features (which for animals means primarily vegetation structure), size of the area, and age and connectivity of the habitats in question. More specifically, the more structurally complex, larger, older, and less isolated a habitat area is, the better the chances for high biological diversity (Cornelis and Hermy 2004; Angold et al. 2006; Chace and Walsh 2006).

In summary, we note, that:

- for highly mobile species, such as birds, structural vegetation diversity is one of the most important factors;
- near-natural vegetation increases robustness and hence resistance to the introduction of invasive species;
- habitat size often correlates to an increase in habitat structures and the variety of microhabitats; it is often also linked to an increase in the number of species, but the positive correlation between species richness and area is a gross simplification;
- habitat age has a variety of aspects comprising pristine remnants, unchanged use and maintenance over decades or even centuries, and succession and emergence of differentiated vegetation structure;
- quality of habitat networks can be described as structural and functional connectivity.

Conclusion

The problem is not, as some scientists suggest, a lack of documentation (Tait et al. 2005) or inadequate understanding of the distribution of individual taxa in specific cities, some of which are documented in great detail. The problem is that the complexity of determinants and the spatial–temporal dynamic of cities (Andersson 2006) preclude simple starting points and lines of argument to explain causal links between biological diversity and cities (Kinzig et al. 2005). If we want to compare cities by appropriate indicators, and if we want to evaluate cities with respect to urban biodiversity, then we need models that help us understand and mirror the causal relationships between urban areas and biological diversity.

The three approaches of embedded cities, urban matrix, and urban patches are suitable for developing applicable models and identifying indicators to monitor and compare the relationship between urban development and urban biodiversity. A specific challenge is to combine the three approaches to a general model of spatial–temporal interactions of urban areas. The three approaches posses the potential to integrate several theories, concepts, and methods, such as hierarchy theory (Whittaker et al. 2001; Wu et al. 2006) and multiscale analysis (Pearson et al. 2004; Schröder and Seppelt 2006), filtering concept (Williams et al. 2009), local–regional species pool process (Collins et al. 2002; Koleff and Gaston 2002), patch-matrix model (Verbeylen et al. 2003; Franklin and Lindenmayer 2009), and rural–urban gradient analysis (McDonnell et al. 1997; McKinney 2008).

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