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Abstract. Urban areas harbour diverse nature ranging from semi-natural habitats to wastelands, parks and other highly human-influenced biotopes with their associated species assemblages. Maintenance of this urban biodiversity for the residents and for its intrinsic value in the face of increasing population and expanding cities requires that ecological knowledge should be better integrated into urban planning. To achieve this goal understanding of ecological patterns and processes in urban ecosystems is needed. The first step in the necessary urban ecological research is to find out what kind of nature exists in cities. Second, knowledge about ecological processes important in urban nature is required. Although ecological processes in cities are the same as in rural areas, some of them, such as invasion by alien species, are more prevalent in urban than in rural conditions. Third, based on ecological knowledge, management schemes maintaining the diversity of urban nature should be designed. These procedures should also include protection of urban nature, e.g. in urban national parks. Finally, as ecology alone cannot provide the complex information about human influence on urban ecosystems, interdisciplinary research involving natural and social sciences is imperative for a holistic approach to integrating ecology into the process of urban planning.

Key words: urban biodiversity, urban ecology, urban planning

Introduction

The proportion of the world's human population living in cities is expected to surpass 60% by the year 2005 (Douglas 1992). Consequently, the management of urban green areas is an increasingly important issue. Urban biodiversity is essential for residents as recreational areas, and their presence in the neighbourhood is an appreciated characteristic reflected in property prices (Tyrväinen 1997).

In addition to being important for residents, urban green areas have intrinsic ecological value. The diversity of human activities in cities creates and maintains a variety of habitats ranging from fairly natural ones to highly modified ones some of which do not occur elsewhere. Thanks to this richness of habitat types, urban landscapes often have a high species diversity even including rare and threatened species (Shepherd 1994). For instance, Eversham et al. (1996) reported that manmade habitats (such as roadsides, colliery spoil heaps, and limestone quarries) support as many as 35% of the rare carabid species in Britain.

Alternatively, urbanization is a threat to many natural habitats and species. For example, over 180 plant species have gone locally extinct in the past 100 years in the German city Munich (Duhme and Pauleit 1998). To counteract these adverse effects of urbanization, and to ensure that urban expansion proceeds sustainably, ecological knowledge needs to be considered in urban planning. However, in many countries, including Finland, there is a scarcity of such knowledge, and the incorporation of ecological information into urban management and planning is weak (Douglas 1992; Sukopp and Numata 1995).

The lack of urban ecological knowledge is not without consequence. First, biodiversity of urban habitats is poorly documented in many cities, and thus baseline information is scarce. Second, as a result, the possibilities of applying ecological knowledge in urban planning are limited. This unsatisfactory situation has been recognized by planners, managers and concerned citizens who regard the use of scientifically gathered ecological information an integral tool in urban planning (Haila 1995).

In this paper, my aims are to (1) examine the theoretical background of urban ecology, (2) investigate characteristics of urban ecosystems, (3) assess what kind of knowledge of urban ecosystems is needed for urban land-use planning, and (4) discuss the importance of maintaining biological diversity in cities as a vital part of nature conservation strategies.

What is urban ecology?

In order to define the concept 'urban ecology' the constituent words 'urban' and 'ecology' need to be discussed. 'Urban' refers to a certain kind of human community with a high density of people, their dwellings and other constructions. A useful distinction between the various types of land-uses, according to the intensity of human influence, was made by Forman and Godron (1986) who divided landscapes into five broad types spanning the continuum from pristine natural environments to urban centres highly modified by people.

At the pristine end of the gradient, natural landscapes support a matrix of mostly unplanted and unmanaged native biota. The next type, the managed landscape, consists of planted and/or managed native or non-native species. In the middle of the gradient, cultivated landscapes have a matrix of agricultural lands that can be either crops or grazing land. The suburban landscapes include low- to moderate-density housing, yards, and roads. The urban end of the gradient represents the most intense human influence, and these landscapes have a matrix dominated by high-density residential and commercial buildings, roads and other paved surfaces. Despite obvious differences, all these land-use types may include patches of other types (Forman and Godron 1986). This urban-to-rural gradient forms a fruitful concept for examining ecological effects of the intensity of human influence on biota (McDonnell et al. 1997).

The meaning of the word ‘ecology’ has expanded during the recent decades (Egerton 1993). More specifically, Haila and Levins (1992) recognize four different meanings of the term. Ecology the *science* investigates nature’s ‘economy’ (flows of matter and energy or distribution and abundance of organisms), while ecology as *nature* is seen as the resource base for humans. Ecology the *idea* is a concept that views human existence in relation to ecology the science (‘human ecology’) and ecology the *movement* refers to political activities related to ecological and environmental issues (the ‘green’ movement).

It is important to recognize that those who are not ecology-scientists often consider ecology to be closer to the three latter definitions than to the first, science-oriented one. Thus, an ecological way of planning and managing urban areas is for many people a combination of several kinds of ecologies, and they all have to be taken into consideration. This makes the integration of ‘ecology the science’ into land-use planning a challenge (Trepl 1995).

As both ‘ecology’ and ‘urban’ have several meanings, ‘urban ecology’ is a diverse and complex concept with different dimensions. For instance, the North American and European use of ‘urban ecology’ differ. In Europe, urban ecological research has traditionally focused on the biota, especially flora, of urban areas, while North American research has been oriented towards social sciences (Wittig and Sukopp 1993). On the other hand, the North American urban ecological research has also included ecosystem fluxes and processes (Pickett et al. 1997b).

These different approaches to urban ecological research indicate that urban ecology is a broad discipline, and it can be defined as ecological research in the urban setting (Rebele 1994). In addition to a scientific component, urban ecological studies usually aim at explicit applications of research in the planning and management of urban green areas (Wittig and Sukopp 1993). Thus, urban ecology is by nature an applied science.

It appears that both research and its applications would gain from collaboration between the social science oriented and natural science oriented approaches to urban ecology (Blood 1994). Ecological research and its applications, such as establishment of protected areas, would benefit from the input of knowledge of human actions in urban areas, while the development of residential areas that maintain and improve the quality of life, health, and well-being of urban residents would benefit from better understanding of urban ecosystems.

Diversity and characteristics of urban biotic communities

Why study urban ecosystems?

Traditionally, ecologists have been reluctant in studying urban nature because it has been regarded as less worthy than non-urban nature (Gilbert 1989; McDonnell and Pickett 1993; McDonnell 1997). However, ecological studies in the urban setting are of value for several reasons.

First, as most people live in urban areas (50% worldwide, 80% in industrialized countries), urban nature is important for recreation and the well-being of residents (Vandruff et al. 1995). In order to create healthy and pleasing environments for them, ecological knowledge of the effects that humans have on urban ecosystems is imperative.

Second, in urban areas, ecological processes are comparable to those outside them (Sukopp and Numata 1995; Walbridge 1997). On the other hand, some ecological processes, such as invasion of species, may be more prevalent in urban environments than in natural ones (Trepl 1995). In addition to population biology, ecosystem processes are an important study area in the urban setting. For instance, rates of certain ecosystem processes appear to be higher in urban than in rural sites. Pouyat et al. (1997) reported that both mass loss and nitrogen release from litterbags reached their maximum in urban oak stands, and net N-mineralization rates were much higher in urban than in rural stands. Litter fragmentation by earthworms and higher soil temperatures in urban sites are potential causes of these differences. In addition to providing insight into the functioning of ecosystems, this kind of information is of vital importance for planning and management purposes.

Third, the considerable variation in urban habitat types and their species diversity has been poorly documented, and finding explanations for the phenomena and predicting changes as urbanization proceeds are challenges for ecological research. In fact, urban nature has be regarded as a field experiment about human impact on ecosystems (McDonnell and Pickett 1990; Haila and Levins 1992). These experiments are usually unplanned from an ecological point of view but can be used to examine ecological principles in urban environments (McDonnell and Pickett 1993).

Trepl (1995) proposed three main properties that distinguish urban landscapes from natural ones, and that may help explain patterns observed in the urban settings: (a) integration (organization, connectivity) among urban habitat patches and communities in them, (b) succession, and (c) invasion by alien species. In addition to these, the question of ecological scale needs to be considered when examining the attributes of species diversity patterns in urban landscapes. In the following, I will discuss these three properties and the question of scale.

Integration among urban habitat patches

The integration among habitat patches and their species communities is often low in cities. Patches are isolated from each other by a matrix of built environment making dispersal difficult and risky at least for poorly dispersing organisms (Gilbert 1989). For instance, Davis (1978) noted that the best predictor of species richness of ground arthropods in London gardens was the proportion of green areas within a 1 km radius of the sampling site.

The approaches of studying the integration of urban habitats include island biogeography and metapopulation dynamics (Trepl 1995). For example, Klausnitzer (1993) provided several examples of the positive relationship between species richness and the area of the habitat patch as would be predicted from the classical island biogeography theory. Similarly, Weigmann (1982) noted that species richness of several groups of arthropods correlated positively with the size of the habitat patch.

Although the theory of island biogeography is very appealing for planning purposes due to the clarity of its basic principles, the SLOSS controversy (i.e. whether Single Large Or Several Small reserves is better for conservation purposes) indicates that it gives no direct indication for the design of nature reserves (Duhme and Pauleit 1998). Furthermore, urban habitats are quite different from true islands for several reasons. First, in the urban setting there is usually no evident mainland to serve as a source area. Second, in cities the matrix may not be as hostile as water surrounding oceanic islands because there are networks of habitat patches enhancing species dispersal in an urban area. Despite these shortcomings, the theory of island biogeography may serve as a first exploration of the relationship between species richness and characteristics of urban habitat patches. However, useful ecological information for planners and managers must include more precise knowledge about species composition and population sizes (Duhme and Pauleit 1998).

Integration of urban habitat patches can be enhanced by creating connectivity, such as corridors and greenways. Noss (1993) provided recommendations for the design of greenways for wildlife conservation. First, greenways should be designed and managed for native species. This will require consideration of the needs of species sensitive to fragmentation and human disturbance over the needs of introduced and opportunistic species that tolerate or thrive in urban landscapes. Second, the planning unit should be the minimum area necessary to insure demographic and genetic survival of the species. Naturally, the spatial scale will vary depending on the area requirements of the focal species. Third, greenways and corridors should not substitute for the protection of large, intact nature reserves in the urban or suburban landscape. For instance, it was clearly demonstrated by Halme and Niemelä (1993) that only large, continuous forest tracts can maintain populations of the most sensitive forest carabid beetles.

Invasion of urban habitats by species

Invasion or movement of individuals between habitat patches is closely associated with integration of communities and patches in the urban setting. The degree that urban habitat patches appear isolated from each other varies from species to species. For birds the built environment between green patches within a city is not a dispersal barrier, while for less mobile species such an environment may be insuperable. In addition to dispersal ability, the habitat requirements of species affect their distribution in urban environments. Thus, a combination of good dispersal ability and wide habitat requirements may be an advantage in urban environments (Gilbert 1989).

Invasion can also be regarded as the colonization of urban nature by non-native species. Increased travel and cultivation of exotic species, e.g. in gardens, have increased the frequency of species introductions (Rebele 1994). Successful invasions by alien species are more common in strongly human-modified habitats than in natural habitats. For instance, in Berlin the proportion of alien plant species increased from 28% in the outer suburbs to 50% in the built-up centre of the city (Sukopp et al. 1979). Studies along a 140 km urban-rural environmental gradient starting in New York City showed a high earthworm biomass (2.16 g worms/m^2) and abundance (25.1 worms/m^2) in urban forests, as compared to rural forests (0.05 g worms/m^2, 2.1 worms/m^2) (McDonnell et al. 1997). This was caused by the occurrence of introduced species in the urban sites. Another example of successful invaders is insects. For instance, in western Canada, the 20 ground beetle (Carabidae) species of European origin are synanthropic (Spence and Spence 1988), and make up the majority of carabids in cities (Niemelä and Spence 1991). Although introduced species add to the diversity of urban species richness, they may depress populations of native species (McDonnell et al. 1993).

Succession and abiotic conditions in urban habitats

Many urban habitats are kept at an early successional stage by regular disturbance, such as mowing. It is also common in urban areas that a part of the biotope represents an early successional stage (e.g. mown lawn) while another part is at climax stage (e.g. old trees). Furthermore, the patchy distribution of urban habitats, combined with a varying degree of human-induced disturbance and chance, results in a number of succession paths across habitat patches. Even adjacent patches may exhibit very different succession paths depending on the colonization history of plants which is to a great extent determined by chance events (Gilbert 1989). This historical uniqueness and overwhelming external control of succession is an important feature distinguishing urban habitats from more natural ones (Trepl 1995).

Also, several abiotic factors differ between urban and rural areas, temperature being one of the most important ones. Many species requiring high temperatures thrive in cities due to higher temperatures there than in the surroundings (Gilbert 1989). This 'heat island effect' can be quite considerable. For instance, in the midlatitudinal United States, average temperatures are approximately 1–2 °C higher in urban areas than in rural ones during winter, and 0.5–1.0 °C higher during summer (Botkin and Beveridge 1997). However, the heat island effect may be unfavourable to some native species, such as snails, that cannot tolerate the increased temperatures (Baur 1994).

Causes of high species richness in urban landscapes: the question of scale

Species richness in single habitat patches (alpha-diversity) is often high in urban habitats. A contributing factor is that many species of different origins find suitable conditions in the anthropogenic habitats. For instance, the area of wastelands and semi-natural grass-herb forests is approximately the same in Vantaa, southern Finland, but the number of vascular plant species is much higher in wastelands (412 species) than in the grass-herb forests (262). The reason is that, in addition to slightly higher number of native species, wastelands harbour more immigrant species than do grass-herb forests (Ranta et al. 1997) (Table 1). Similarly, Gödde et al. (1995) reported that highly disturbed sites, such as wastelands and gravel pits, had the highest species richness of vascular plants, butterflies, grasshoppers, landsnails and woodlice in the city Düsseldorf, Germany.

However, for some groups of organisms urban conditions are not favourable. Lawrynowicz (1982) reported that in the Polish city Lodz species richness of macro-fungi in parks decreased from 185 species in the suburban zone to 86 species in the less densely built urban zone, and to 38 species in the urban core of the city. Also Pouyat et al. (1994) reported that abundance of fungi in forest patches increased with distance from New York City towards its rural surroundings along a 140 km long transect.

The high total species richness of an urban landscape is a result of high alpha-diversity and variation in species communities between patches (beta diversity). The considerable variety of habitat types and their associated species communities in urban areas leads to high beta-diversity (Rebele 1994). For instance, in the Helsinki area, variation in community structure of plants was higher among urban habitats (various kinds of parks and wastelands) than among semi-natural forest sites outside the city (Tonteri and Haila 1990). Similarly, Czechowski (1982) noted that the similarity of carabid communities

Table 1. Number and proportion (%, in parenthesis) of vascular plant species of different origin in wastelands (highly human-influenced habitat) and grass-herb forests (semi-natural habitat) in Vantaa, southern Finland.

Origin of species	Number of species	
	Wasteland	Grass-herb forest
Native species	204 (49)	187 (72)
Introduced species		
Archaeophytes	103 (25)	42 (16)
Neophytes	68 (17)	22 (8)
Cultivation escapes	37 (9)	11 (4)
Total number of species	412	262

Source: Ranta et al. (1997).

was low (46% on the average) among urban forest patches probably due the poor dispersal ability of forest-dwelling species.

In addition to invasion, patchily occurring local extinctions maintain variation in species composition among urban habitats (Rebele 1994). Extinctions occur due to habitat destruction or slow disappearance of species from patches that have been fragmented into small and isolated remnants. While there is ample evidence of species going locally extinct due to habitat destruction (e.g. Gilbert 1989), extinction due to isolation and/or decreased size of the habitat patch are more difficult to show.

However, the effects of patch size and habitat change may be difficult to distinguish. For example, Halme and Niemelä (1993), (see also Niemelä and Halme 1998) reported a high number of carabid species in small forest fragments (0.5–3.0 ha; 17.6 species in a standardized sample) surrounded by agricultural-urban areas as compared to large ones (9.6–21.5 ha; 12.8 species) or continuous forest (11.2 species). This was due to invasion of species from the surrounding grassland habitat. This in turn was attributed either to easier invasion of the small fragments or to such differences in habitat structure that make the small fragments suitable habitat for the grassland species. The latter hypothesis was supported by vegetation analyses showing that plant species composition (trees excluded) of the small fragments was more similar to the surrounding grasslands than to large forest patches or to continuous forest.

In conclusion, the low degree of integration among habitat patches leading to variation in colonization and extinction events together with their early to mid-successional stage caused by frequent disturbances making them suitable for many species may explain the high species richness in urban areas. Furthermore, it appears that the 'intermediate disturbance hypothesis' (Connell 1978) stating that diversity is highest in slightly disturbed habitats is applicable in urban landscapes. For instance, Blair and Launer (1997) showed that species richness and Shannon diversity of butterflies peaked at moderately disturbed sites across a rural-urban gradient. Also Jokimäki and Suhonen (1993) demonstrated that species number of birds was higher in lightly disturbed sites (villages and countryside; 18–22 species/50 pairs) and in natural forests (18 species/50 pairs) than in centres of cities (7–12 species/50 pairs).

Ecology and urban planning

There are three broad questions that need to be addressed in order to incorporate ecological knowledge such as outlined above into urban planning.

First, we need to know what kind of nature exists in urban areas. In many cities, this basic ecological knowledge is still scarce. A method for assessing the occurrence of various habitat types, and associated species in an urban landscape is biotope mapping (Wittig et al. 1993). This method has been developed and refined in central Europe, especially Germany, where today it is used routinely (Sukopp and Weiler 1988). Biotope mapping produces information about the physical properties, such as location and size, and about biotic characteristics, such species composition, of biotope patches found in a city. This information can be presented as maps and databases, and forms a useful basis for urban planning (Sukopp and Wittig 1993).

Second, knowledge about processes affecting urban nature in comparison to rural nature would both improve our understanding of urban ecosystems, and help planners and managers in their work. Some of the important processes differing between urban and rural landscapes have been discussed above. Especially the significance of human-induced disturbances, and the consequent effects on succession merit more research (Rebele 1994; Trepl 1995). In addition, invasion by alien species, and their interactions with native ones are more prevalent in urban landscapes than in rural ones. These need to be better understood so that the potentially harmful effects of exotic species on native biota can be mitigated.

Third, based on ecological knowledge, ecosystem-specific management schemes need to be designed for urban nature. For instance, 'benign neglect' is a management approach proposed to maintain high species diversity and richness of habitat types in urban landscapes (Haila and Levins 1992). This approach is based on the two features of urban nature discussed above; high alpha and beta diversity. Management prescriptions would include leaving certain areas unmanaged, while some areas would be managed lightly, and yet others more intensively. The variety of site-specific management procedures used would produce a diverse and rich urban green landscape. However, the applicability of the approach has not been properly tested.

Ecology alone cannot provide the complex information that city planners and managers need. An integration of concepts and methods satisfying both natural and social scientists as well as managers needs to be developed (see e.g. Sukopp and Wittig 1993; Pickett et al. 1997a, b). A useful way to operationalize this integration is the urban-to-rural gradient approach (McDonnell and Pickett 1990). The idea is to compare sites with the same original physical environment (e.g. forest patches) but differing in measurable features of urbanization. These gradient analyses have been mainly applied in ecological research but the inclusion of social, economical and cultural components would produce a more holistic view.

Urban biodiversity and nature conservation

How does biodiversity relate to studies in urban ecology and the maintenance of the green urban landscape? Haila and Kouki (1994) defined biodiversity as an inherent property of nature, which maintains natural variation on the various scales of the ecological system. Thus, biodiversity is both the raw material providing the basis for adaptations of ecological systems to their environments, and a buffer that enhances the system's resilience against disturbances. As disturbance is one of the key issues in urban landscapes, the relationship between diversity and resilience is of particular importance here. For instance, in Finland, it has been noted that as disturbance in the form of trampling increases, plant species composition of urban forests changes to include more introduced species and trampling tolerant native species (Ranta, P. unpublished results). To what extent these changes depend on the initial diversity of forest vegetation is currently being investigated.

As biodiversity is an inherent property of ecological systems at various spatial and temporal scales, an approach to research and management encompassing the different levels of diversity is needed. Therefore, maintenance of biodiversity from populations to ecosystems is a useful guiding principle of urban planning. An important aspect of the maintenance of biodiversity is setting aside green areas as a vital part of nature conservation strategies. One justification for nature protection in cities is that many urban habitats are unique, and not found elsewhere. Many of these habitats have high species richness, and harbour even threatened species. However, high density of the human population in cities and the consequent need for recreational areas makes traditional nature conservation with strictly protected areas difficult. A solution may be a policy that recognizes the strong human presence in urban nature, and tries to find a compromise between protection and sustainable use of nature. For instance, it has been suggested that urban national parks including suburban and agricultural areas, in addition to natural habitats should be established. These parks could include protected areas of different degrees including recreational areas. Maintenance of a diverse green environment is imperative for the well-being of humans as well (Vandruff et al. 1995; Tyrväinen 1997). Urban national parks would also raise the status of urban nature, and enable city residents to familiarize themselves with the rich urban ecosystems.

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