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Is there a need for a theory of urban ecology?

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Abstract. Although urban ecosystems are governed by the same ecological "laws" as rural ecosystems, the relative importance of certain ecological patterns and processes differs between the two types of ecosystems. For instance, as compared to rural areas, urban habitats are usually more islandlike, more often represent early successional stages, and are more easily invaded by alien species. All these features are results of the intense human influence on urban landscapes. The question then arises whether a distinct theory of urban ecology is needed for understanding ecological patterns and processes in the urban setting. The answer is no, because urban ecosystems can be successfully studied using existing ecological theories, such as the metapopulation theory. However, due to the intense human presence, approaches that include the human aspect are useful in studying urban systems. For instance, the "human ecosystem model," which emphasizes human impact by identifying social components with connections to ecology, is a useful approach in urban studies. This model, combined with the urban–rural gradient approach, forms an effective tool for studying key ecological features of urban ecosystems. Better understanding of these features would increase our ability to predict changes that land use causes in urban ecosystems, and would help to integrate ecology better into urban planning.

Keywords: urban ecology, theory, urban planning

Introduction

Traditionally, ecologists have been reluctant to study urban ecosystems, because they have been regarded as inferior to less disturbed rural ones (Gilbert, 1989; Haila, 1999; McDonnell, 1997; McDonnell and Pickett, 1993; Rees, 1997). However, this attitude is changing as ecologists are becoming more aware of and concerned about the effects of humans on ecosystems (Walbridge, 1997). In addition to ecological research in the urban setting becoming increasingly attractive as a scientific endeavor, information produced by such research is becoming important in urban planning (Wittig and Sukopp, 1993).

Expansion of cities and towns is a significant cause of conversion of land to highly human-modified urban landscapes. From an ecological point of view, urbanization can have both favorable and adverse effects on biotic communities. On the one hand, the diversity of human influence in cities creates and maintains a variety of habitats that do not occur elsewhere. This richness of habitat types often supports a high species diversity even including threatened species. For instance, Eversham *et al.* (1996) reported that manmade habitats (such as roadsides and colliery spoil heaps) host as many as 35% of the rare carabid beetle species in Britain. On the other hand, urbanization is a threat to many natural habitats and species. For instance, in the German city of Munich over 180 plant species have gone locally extinct in the past 100 years (Duhme and Pauleit, 2000).

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These examples illustrate that urban ecosystems represent an extreme case of human effect on ecosystems and thereby differ from more natural ecosystems. With this background, my goal is to examine the ecological differences between urban and rural landscapes and whether current theories in ecology are applicable to urban areas. If not, what are the reasons? If so, how specifically can these theories be applied or tested?

Definitions of key terms

Urban ecology is ecological research done in cities and towns. There are many definitions of “urban.” Basically, it is a geographical term characterizing the land use of an area. A broad definition states that an urban area or a city is a fairly large, densely populated area characterized by industrial, business, and residential districts. A quantitative definition provided by OECD states that an urban region is a functional unit in which at least 85% of the inhabitants are urban residents. Urban residents in turn are defined as those who live in an area in which the population density is at least 150 people/km^2 (Lahti, 1997). According to this definition only 20% of the Finnish population lives in urban areas because of the overall low population density in the country. According to other, less stringent definitions of a city, over 80% of the Finnish population lives in cities and towns. For the purpose of urban ecological research the broad definition appears more useful because it is often difficult to draw any definite ecological borders around an urban area. Thus there is a continuum of decreasing human influence from city centers to wilderness. For studying ecological changes along this continuum, the urban–rural gradient approach introduced below forms a useful framework. “Rural” in this paper refers to “nonurban” areas that are outside urban or suburban areas.

Urbanization is the process leading to increasing amounts of urban areas. Urbanization in a broad sense means the conversion of land into urban environments. This process is taking place all over the world, and the proportion of the world’s human population living in cities is expected to surpass 60% by the year 2005 (Douglas, 1992). Thus urban areas are going to cover increasingly large areas in the future. To manage the green spaces of the growing cities is a challenge, but ecological research may provide some answers if the understanding gained is applied in planning and management procedures (Wittig and Sukopp, 1993).

Although ecology is a natural science concerned with the distribution and abundance of organisms, the word has many other meanings as well (Haila and Levins, 1992). Consequently, urban ecology is not necessarily only the natural science of ecology but may include elements from the social sciences. For instance, Rebele (1994) divided ecological research in the urban setting into two broad types: social sciences oriented and ecology oriented. Traditionally, these two approaches to urban ecology have been independent and sectorial (Wittig and Sukopp, 1993). However, it appears that the integration of these two approaches would benefit both parties (Blood, 1994; Rees, 1997). Ecology would benefit from the knowledge of the structure and function of human society in urban areas, while social sciences and planning would benefit from understanding the ecology of urban systems. For instance, in many parts of the world the current lack of ecological understanding of urban ecosystems hampers the incorporation of green areas into residential areas for the maintenance and improvement of the quality of life, health, and well-being of urban residents. Furthermore, the maintenance of the biological diversity of ecosystems in the urban setting requires ecological understanding of the composition and functioning of urban systems.

To integrate the social sciences-oriented and ecology-oriented approaches, Pickett *et al*. (1997a) proposed two ways of increasing socioecological knowledge of urban systems. First, social, cultural, and economic processes should be linked with biological and physical ones in order to understand urban areas as integrated systems. Second, a long-term research perspective is needed because of the temporally dynamic nature of the socioecological urban system.

To summarize, urban ecology is a diverse field of research that forms a continuum from "pure" ecology in the urban setting to a combination of ecology and social sciences to examine urban systems. Thus urban ecological research may emphasize societal or natural sciences, and often seeks to apply research results to urban planning and management. There is a need, as noted by Rees (1997), for urban ecology to converge with human ecology, if we want to achieve global ecological sustainability in our growing cities. The geographical scale of research is often relatively large, spanning a city and its surroundings. Consequently, urban ecological research often takes place at the landscape scale.

Ecology of urban ecosystems

The good, the bad, and the subtle effects of humans

McDonnell and Pickett (1993) divided the effects of human actions on ecosystems into three types. The "bad" effects are obvious negative phenomena such as toxic waste spills, which have been well studied by ecologists. The "subtle" effects include a variety of inconspicuous or indirect interactions of humans with ecosystems. Examples include changes in competitive hierarchies among species due to anthropogenic disturbance or introduction of alien species. Often, subtle effects are historical, such as the current structures of many forests as the results of land-use practices applied centuries ago.

The third kind of human effects are directly associated with areas populated by humans, and are labeled "good" by McDonnell and Pickett (1993), not because all effects of human habitation are ecologically good, but because concentrations of people are apparently socially desirable by humans. Urban areas represent the most densely populated concentrations of people, and these environments can be treated as ecosystems of which humans are an integral part (Walbridge, 1997).

Although concentrations of humans may be good for *Homo sapiens*, cities have profound effects on other species. These impacts may be positive or negative. For instance, 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 German city of Düsseldorf. On the other hand, some groups of organisms suffer from increased urbanization. For example, Lawrynowicz (1982) reported that species richness of macrofungi in parks of the Polish city of Lodz decreased from 185 species in the surroundings of the city to 86 species in the less densely built urban zone, and dropped to 38 species in the urban core.

Owing to these variable responses of species to urban pressure, it has been suggested that urban landscapes can serve as field experiments for addressing both basic ecological questions and issues related to the ecological effects of humans on their environment (Haila and Levins, 1992; McDonnell and Pickett, 1990). The study of urban systems could provide ecological insight into the good, the bad, and the subtle effects of humans on ecosystems that could help minimize the harmful effects of urbanization on other species and ultimately on humans themselves.

Differences between urban and rural ecosystems

It is evident that urban ecosystems are strongly affected by humans, but is the degree of human influence the only difference between urban and rural ecosystems? Walbridge (1997) answered this question by stating that “urban ecosystems differ from their ‘natural’ counterparts solely in the degree of man’s influence.” Other urban ecologists agree (e.g., Gilbert, 1989; Sukopp and Numata, 1995). However, some ecological processes are more prevalent in urban environments than in rural ones. For instance, invasion by alien species is more common in urban than in rural conditions (Elton, 1958; Spence and Spence, 1988). It appears that examining the differences in ecological processes between urban and rural environments is an especially fruitful approach for urban ecological research, and for the subsequent application of the results in urban planning and management of green areas.

Trepl (1995) proposed three main properties distinguishing urban landscapes from rural ones that merit research: (a) patchiness of urban ecosystems and poor connectivity among them, (b) succession, and (c) invasion by alien species. In addition to these, the question of ecological scale needs to be considered when investigating urban landscapes, especially for the attributes of species diversity patterns.

Patchiness of urban ecosystems

In cities, habitat patches are often small and isolated from each other by a matrix of built environment. Specific ecological theories that can be used as a framework for examining ecological patterns and processes in such urban “archipelagoes” include island biogeography theory (MacArthur and Wilson, 1967) and metapopulation theory (Hanski and Simberloff, 1997). For instance, Klausnitzer (1993) provided several examples of the positive relationship between species richness and the area of urban habitat patches 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. However, Schaefer (1982) did not find such a relationship.

These findings of a positive relationship between patch size and species richness suggest that the theory of island biogeography could be an appropriate framework for urban ecological research. However, the controversy termed SLOSS (single large or several small reserves) indicates that island biogeography theory gives no direct guidance for the design of nature reserves or urban green areas (Duhme and Pauleit, 2000). Despite the controversy, the theory may serve as a first exploration of the relationship between species richness and characteristics of urban habitat patches, but useful ecological information for planners and managers must include more than species richness estimates. Precise knowledge about species identity and population sizes is needed (Duhme and Pauleit, 2000).

The patchiness of urban green areas makes dispersal, a central theme of metapopulation theory, difficult and risky at least for taxa with poor dispersal ability. Consequently, the extent of green areas and their connectivity is an important factor affecting species occurrence in urban landscapes. For instance, species richness of ground arthropods in London gardens was determined by their degree of isolation, i.e., the proportion of green areas within a 1 km radius (Davis, 1978). In particular, less mobile species, such as nonflying and ground-dwelling arthropods, have difficulties in dispersing among isolated patches (Gilbert, 1989). The metapopulation theory has not been tested in urban landscapes yet, but it appears to provide a promising framework for urban ecological studies.

Connectivity of urban habitat patches can be enhanced by creating movement corridors and greenways. However, as noted by Noss (1993), greenways and corridors should not substitute for the protection of large, intact nature reserves in the urban or suburban landscape, as such areas are needed for the maintenance of populations of the more sensitive species and as source areas for colonists (Halme and Niemelä, 1993; Niemelä and Halme, 1998).

Invasion, extinction, and succession in urban ecosystems

Increased travel and cultivation of exotic species have increased the frequency of species introductions and invasions into urban areas (Rebele, 1994). Successful invasions by alien species are more common in strongly human-modified habitats than in more natural habitats (Spence and Spence, 1988; Rapoport, 1993). For instance, the proportion of introduced plant species increased from 10 or 20% in rural areas surrounding the city of Bariloche (Argentina) to 100% in the city center (Rapoport, 1993). Although introduced species add to the diversity of urban species richness, they may depress populations of native species (McDonnell *et al*., 1993).

In addition to invasion, frequent local extinctions maintain variation in species composition among urban habitat patches (Rebele, 1994). Extinctions take place rapidly due to habitat changes or slowly as "species relaxation" (slow disappearance of species from habitat fragments). While there is ample evidence of species going locally extinct due to habitat change (e.g., Gilbert, 1989), relaxation due to isolation and/or decreased size of the habitat patch are more difficult to show. Furthermore, decrease of patch size may be associated with habitat changes, and it may thus be difficult to pinpoint the exact cause of species decline (Niemelä and Halme, 1998).

Another typical feature of urban habitats is their early successional stage, which is maintained by disturbance, such as regular mowing of parks. Furthermore, successional development is highly variable in urban green spaces. The patchy distribution of urban habitats results in stochastic colonization events which, when combined with varying degrees of human-induced disturbance, lead to a diversity of successional paths among habitat patches. Even adjacent patches may exhibit very different successional 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 less human-influenced ones (Trepl, 1995).

Scales of variation in urban landscapes

Species richness in single-habitat patches (alpha diversity) is often high in urban habitats because many species of different origins find suitable conditions in them. For instance, the number of vascular plant species was much higher in wastelands (abandoned heaps of soil, abandoned lots, etc.) and ruderal sites (412 species) than in seminatural coniferous grass–herb forests (262 species) of approximately equal area in the Finnish city of Vantaa (Ranta *et al*., 1997). The reason was that, in addition to a slightly higher number of native species, wastelands and ruderal sites harbored more immigrant species (171) than did forests (64).

Also the landscape-level species richness is often high in urban settings. This is due to variation in species composition among patches (beta diversity), which in turn is a result of a high variety of habitat types ranging from seminatural to highly anthropogenric ones (Rebele, 1994). For instance, in the city of Helsinki, beta diversity of plants was higher among urban habitats (various kinds of parks, ruderal sites, and wastelands) than among seminatural forest sites outside the city (Tonteri and Haila, 1990). Similarly, in Berlin, variation in invasion events and habitat quality caused considerable differences in carabid species composition among habitat patches, which led to high beta diversity (Kegel, 1990).

In summary, isolation of urban habitat patches leads to variation in colonization and extinction events. This factor, together with the early to mid-successional stage caused by disturbances, contributes to the high species richness in urban landscapes. Thus it appears that the “intermediate disturbance hypothesis” (Connell, 1978) predicting that species richness is higher in intermediately disturbed sites than in heavily disturbed or undisturbed ones is applicable in urban landscapes. For instance, species richness and diversity (measured as Shannon diversity index) of butterflies peaked at moderately disturbed sites across an urban–rural gradient in California (Blair and Launer, 1997), and carabid species richness was highest in intermediately disturbed sites along an urban–rural gradient in England (Spence, 1990). Also the number of bird species was higher in lightly disturbed sites such as villages and countryside (18–22 species) than in natural forests (18 species) or city centers (7–12 species) in Finland (Jokimäki and Suhonen, 1993). Furthermore, Haila *et al*. (1989) showed that ground-dwelling arthropod fauna had a low diversity in frequently disturbed urban habitats, such as mown park lawns.

Need for a theory of urban ecology?

Trepl (1995) felt that a new theory of urban ecology, or at least a framework within which urban ecological research could be conducted, was needed. Such a theory, or framework, would need to deal with the structure and functioning of urban ecosystems, i.e., the theory would have to identify the specific features (such as invasion, disturbance) of urban ecosystems, and distinguish them from other ecosystems. Although there are differences between urban and rural ecosystems, as I have shown, it appears that the basic ecological patterns and processes are similar. The main difference seems to be the relative importance and prevalence of certain processes in urban as compared to rural landscapes. This being the case, no need exists for a distinct theory of urban ecology. The existing ecological theories can be applied when studying ecology in the urban setting. The most promising ones are those that address the special features of urban ecosystems (isolation, succession, disturbance) and include the island biogeography theory, the metapopulation theory, and the intermediate disturbance hypothesis.

Due to the overwhelming influence of humans on urban ecosystems, a fruitful approach to a holistic view of urban ecosystems is an integration of concepts and approaches satisfying both natural and social scientists, as well as managers. A useful approach to combine these elements is the "human ecosystem model," which identifies several social components and processes where connections to ecological fluxes, processes, and structures exist (Pickett *et al*., 1997b). The model consists of a human social subsystem and resources subsystem. The human subsystem includes social institutions, social cycles (e.g., physiological, individual, and environmental), and social order, while the resources subsystem comprises both human resources (cultural and socioeconomic resources) and ecosystem resources (ecosystem patterns and processes). All the major subsystems are functionally linked. The human ecosystem model provides a framework for urban ecological studies addressing questions of varying specificity. However, the specific ecological theories within the model can be the same for both urban and nonurban areas.

Pickett *et al*. (1997b) proposed that the urban-to-rural land-use gradient could serve as a model system for the study of the responses of biotic communities to human disturbance (see also McDonnell *et al*., 1997; Niemelä *et al*., 1999). The idea is to compare sites with the same original physical environment (e.g., forest patches) but differing in measurable features of urbanization from city centers to their rural surroundings. Until now gradient analysis has been mainly applied in purely ecological research, but the inclusion of social, economic, and cultural components would produce a more holistic view as emphasized by the human ecosystem model. The combination of this model and gradient analysis to studies of the special properties of urban ecosystems (isolation, invasion, and succession) would seem to form a fruitful approach to urban ecological research. Specific ecological hypotheses to be tested could include, for instance, the metapopulation theory.

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