Local Management and Landscape Effects on Diversity of Bees, Wasps and Birds in Urban Green Areas

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Abstract

Today almost all ecosystems on Earth are directly or indirectly influenced by human activity. Most species occur in ecosystems that are managed by humans and only a small fraction of biodiversity exists in protected areas. Therefore, human dominated areas must also be considered for conservation of biodiversity.

I have studied the effect of urbanization and green area management on bumble bees, compared the effects of urbanization and agriculture on trap-nesting insects, and also included how management practices and landscape changes through urbanization affect birds. Further, the social drivers behind management practices of three different types of urban green areas (cemeteries, city parks and allotment gardens) were studied through interviews with managers. I also interviewed local managers of allotment gardens to get their perspective on the management.

I found that diversity of bumble bees, trap-nesting insects, and birds decreased with urbanization, whereas bumble bee abundance and species composition, and bird species composition, were most affected by local management and habitat quality. Allotment gardens had much higher abundances of bumble bees than city parks and cemeteries. Management practices differed among the three types of green areas and were most affected by social organization, local ecological knowledge and sense of place of the managers. Both local ecological knowledge and sense of place were more pronounced among allotment gardeners. Among the allotment gardeners the most important social drivers were that the management was meaningful and very important for their well-being.

To favour bumble bees, trap-nesting insects, and birds within cities it is important to improve the qualities of urban green areas as habitat for these species. Further, it is important to maintain a variety of green areas within the city, and to enhance the connectivity among green areas within the city and with habitats in the hinterlands. Planners should recognize urban green areas that are normally overlooked in green plans of the city, such as allotment gardens. These areas have a large potential for biodiversity conservation within cities.

Keywords: urbanization, bumble bees, *Bombus*, trap-nesting insects, birds, management, allotment gardens, cemeteries, city parks, conservation, urban-rural gradient

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”Nog finns det mål och mening i vår färd - men det är vägen, som är mödan värd…”

Karin Boye

Contents

List of publications

The present thesis is based on the work contained in the following papers, referred to by Roman numerals:

I Andersson, E., Ahrné, K. Pykkönen, M. and Elmqvist, T. Patterns among urbanization measures in Stockholm, Sweden, and their ecological implications. (Submitted manuscript).

II Andersson, E., Barthel, S. and Ahrné, K. (2007). Measuring social-ecological dynamics behind the generation of ecosystem services. *Ecological Applications* 17(5), 1267-1278.

III Ahrné, K., Bengtsson, J. and Elmqvist, T. Bumble bees and urbanization: patterns of diversity, abundance and flower visitation. (Submitted manuscript).

IV Ahrné, K. and Bommarco, R. Landscape effects of agricultural intensification and urbanization on trap-nesting bees and wasps. (Manuscript).

Introduction

Human activity and biodiversity

Humans are the dominating species on Earth and today almost all parts of the Earth's surface are directly or indirectly influenced by human activity (Vitousek et al., 1997). Most species occur in ecosystems that are managed by humans in one way or the other and only a small fraction of biodiversity exists in protected areas (Pimentel et al., 1992; Hoekstra et al., 2005). Also, the biological diversity in protected areas is dependent on the land use of the surrounding landscape (Pimentel et al., 1992; Bengtsson et al., 2003). Biological diversity is suggested to be important for the stability of ecosystem functioning in case of disturbance, the resilience of the ecosystem (e.g., Elmqvist et al., 2003) and also as insurance for future generations (e.g., Ehrlich & Wilson, 1991). Humans are dependent on goods and services provided by other species and through species interactions within ecosystems (Daily, 1997). Historically ecologists and conservation biologists have tended to focus on areas with relatively small human presence (Worster, 1994; Miller & Hobbs, 2002). However, if we are to conserve and utilise biological diversity in a sustainable way, which is the objective of the Convention on Biological Diversity (http://www.cbd.int/) now signed by 168 countries, we need to do this also in areas dominated by human activities. Conservation and restoration of native habitats in densely populated areas also have social, recreational and educational value (e.g., Niemelä, 1999; Miller & Hobbs, 2002).

Among the human activities that have altered ecosystems and their functions the most are urbanization and agricultural intensification (McKinney, 2002; Ricketts & Imhoff, 2003). The main focus of this thesis has been on urbanization and its effect on pollinating insects, but I also investigate the effects of urbanization and agriculture on trap-nesting insects (*Paper IV*).

Urbanization

Today half of the human population lives in urban areas (UN, 2007) and the urban populations are predicted to increase in the future, both because of an overall human population increase and because people are moving from rural to urban areas. In the more developed countries of the world (as defined by the UN) 74% of the population now lives in urban areas, and is predicted to increase to 86% until 2050 (UN, 2007). Whereas in less developed countries 44% of the population lives in urban areas and is predicted to increase to 67% in the same period of time (UN, 2007). Therefore urbanization is a process that is likely to continue and increase in the future. Urbanization causes drastic and persistent changes of the landscape and the environment (McKinney, 2006) and although urban areas only cover a small proportion of the Earth's surface, somewhere between 1% and 6%, they make use of a large proportion of the Earth's natural resources (Alberti et al., 2003). Cities are mainly dependent on goods and services produced elsewhere to support their large populations (Folke et al., 1997), their "ecological footprint" may be ten to hundred times larger than their actual areas, (Collins et al., 2000; Alberti et al., 2003). The cities also produce waste products that need to be taken care of which influence ecosystems on a global scale. Cities are responsible for 78% of the global carbon emissions, 60% of residential water use and 76% of the wood used for industrial purposes (Grimm et al., 2008).

Cities can be seen as the endpoint of human domestication of landscapes, and what happens to ecosystems in urban areas today may appear in other areas in the future (Karieva et al., 2007). Locally, cities can be viewed as large-scale experiments on the effects of global change on ecosystems (Carreiro & Tripler, 2005). Because significant warming, increased nitrogen deposition, and human domination of ecosystem processes are already prevalent in urban environments (Carreiro & Tripler, 2005). Therefore, studying urban ecosystems may reveal information of human effects on ecosystems, which could be used for predicting future changes elsewhere. As humans dominate urban ecosystems, they set the stage for all other species present (Alberti et al., 2003), most obviously, perhaps, through physical changes of the landscape accompanying the construction of, e.g., buildings and roads. Such transformations of the landscape are also likely to be persistent over time (McKinney, 2006). Once an area is built up or made hard it continues to stay this way for a long time. Urbanization is not uniform and does not occur in the same way all over the world. All cities have their unique characteristics and different ways of expanding. Their influence on biodiversity will depend on many factors not least where they are situated (e.g., Ricketts & Imhoff, 2003). However, cities also contain similar elements as they are created to meet the needs of mainly one species, our own (McKinney, 2006).

In general, urbanization reduces species richness within cities (Grimm et al., 2008). But there are exceptions to this pattern, for example plant species richness often increase in urban areas compared to wilder areas (Grimm et al., 2008). In this case also plant species introduced and planted by humans are included. Plant communities in urban areas are perhaps more directly controlled and dependent on human decisions than any other organism group (Hope et al., 2003; Grimm et al., 2008). Hope et al. (2003) found that plant diversity was influenced by the socioeconomic status of the urban dwellers. Further, studies have found bird and butterfly species richness to peak at intermediate levels of urbanization (Blair, 1996; Blair & Launer, 1997; Marzluff, 2005). For bees there is some evidence that abundance and species richness may be higher in areas moderately modified by human activity than in more undisturbed natural habitats (Winfree et al., 2007). However, in general, bee species richness within cities is lower than in nearby wilder habitats (e.g., McIntyre & Hostetler, 2001; Eremeeva & Sushchev, 2005; Matteson et al., 2008).

To only focus on species richness in conservation, without knowledge about the identity of the species, may be misleading. Species identity and composition is often more important for the functions of the ecosystems (Kremen, 2005). Urbanization tends to alter the species composition of communities in urban areas compared to those in the surrounding landscape (Grimm et al., 2008). For example, bee communities within the city of New York consist of more cavity nesting and non-native species than in the region at large (Matteson et al., 2008). Birds often shift to more granivorous species at the expense of insectivorous species (Grimm et al., 2008), and among arthropods herbivorous species seem to be more abundant in cities, whereas parasitoids show the reverse pattern (reviewed in McIntyre, 2000). The similarity of green areas in cities and those in the surrounding landscape also influences species richness and composition within urban green areas.

In Phoenix, which is situated in the desert, xeriscaped gardens had more bee species than mesiscaped gardens (McIntyre & Hostetler, 2001). Also, Blair & Launer (1997) suggest that to maintain the original communities, of butterflies, in urban areas the undeveloped land should be kept in as natural state as possible. McKinney (2006), argue that cities are surprisingly similar to each other in terms of flora and fauna independently of geographical and climatic differences. For example, among 321 alien plant species found in the city of Braunschweig, more than 80% were also found in Berlin, Vienna and London (Sukopp, 1990). Some species such as pigeons and rats profit from human settlements while most species are negatively affected. Still, urban areas may be heterogeneous environments that provide habitat for many species of, e.g., bees (Saure, 1996; Tommasi et al., 2004; Frankie et al., 2005; Matteson et al., 2008) and other insects (Frankie & Ehler, 1978).

Green areas within the city may also have important educational values. Increasing urbanization leads to a disconnection of humans from nature, called the "extinction of experience" (Pyle, 2003). For many people in larger cities, urban green areas are their only contact with nature. This contact may actually be crucial for their understanding of natural ecosystems and in turn their willingness to preserve biodiversity also elsewhere (Miller, 2006). Meaningful interactions with nature nearby from an early age increase people's awareness of ecological processes and functions (Miller, 2005). Since a large part of the human population lives in urban areas, their interest in and knowledge about natural ecosystems will have an important influence on political decisions regarding biodiversity conservation.

Ecosystem services

Daily (1997), defined ecosystem services as:

> …the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life.

Some examples of ecosystem services are: pollination of cultivated crops and wild plants, biological control of pest species, seed dispersal, purification of air and water, detoxification and decomposition of wastes, and a provision of aesthetic beauty (Daily, 1997). Thus, ecosystem services are services provided by natural ecosystems that are essential for human survival, and that increase the well-being of people. Kremen & Ostfeld (2005) highlighted the importance of understanding how human activity affects the species and functional groups that provide these services. Pollinator declines, mainly due to human activities, affect the yield of insect pollinated crops and the quality of the harvest (Allen-Wardell et al., 1998, Steffan-Dewenter et al., 2005). Green areas in cities may provide a multitude of other ecosystem services, such as air filtering, micro-climate regulation, noise reduction, rainwater drainage, and also have recreational/cultural values for humans (Bolund & Hunhammar, 1999).

Pollination

The importance of pollination as an ecosystem service is perhaps mostly associated with the agricultural landscape. Several studies have found that the yield of insect pollinated crops increase with increasing diversity and abundance of pollinator species. In a review of the importance of pollinators for world crops Klein et al. (2007) found that 87 of the leading global food crops are entirely or partly dependent on animal pollination and that these crops make up 35% of the global food production. The fruit set of highland coffee in an agroforestry system in Indonesia increased with increasing bee diversity (Klein et al., 2003). The diversity of social bees was negatively related to distance to rainforest and the diversity of solitary bees was positively related to light intensity within the agroforestry system (Klein et al. 2003). Also, visitation rate to coffee plants (Ricketts, 2004) and pollen deposition on melon (Kremen et al., 2004) by native bees was higher close to natural habitats than at a larger distance. These results indicate that management, both at a larger landscape scale (through conservation of natural habitats near crops) and at the local scale, affect the ecosystem service pollination. In urban areas in the developed countries, pollination within the city may be important for fruit set of vegetables and fruits cultivated in gardens; thus mainly of recreational value, but also for educational purposes. In other parts of the world, e.g., in many African cities, citizens are more dependent on urban agriculture for food production (Bryld, 2003). Historically, and during the World War I and II, cultivation for food production was considerable also in Swedish cities (http://www.koloni.org/pdf/01.pdf). We risk losing the possibility to adapt to future needs if we ignore the biodiversity of urban ecosystems today. However, most importantly in my view, given worldwide pollinator declines (e.g. Steffan-Dewenter, 2005; Biesmeijer et al., 2006) and the loss of natural habitats for pollinators (Kearns et al., 1998); all potential habitats, also flower rich green areas in cities, need to be considered for the conservation of this essential functional group.

Local and landscape scale

Local species diversity is dependent on regional species diversity and both regional and historical processes influence local community structure (Ricklefs, 1987). Based on landscape ecology (Turner et al., 2001) and metacommunity theory (Leibold et al., 2004) species and communities within habitat patches are predicted to be dependent not only on local conditions, but also on the surrounding landscape and interactions with other habitat patches through dispersal. Dispersal is related to the mobility of different species and how they perceive connectivity among habitats within the landscape (Tscharntke et al., 2005; Lindenmayer et al., 2007). Different species will perceive and react to landscape changes at different spatial scales (e.g. Steffan-Dewenter et al., 2002). Therefore, to understand patterns in species diversity and community composition within local habitats a landscape perspective is needed. This also has implications for management. Habitats cannot be successfully managed as independent entities; instead managers, ranging from farmers to governments, need to consider whole landscapes (Bengtsson et al., 2003; Lindenmayer et al., 2007). To be able to predict the effects on biodiversity of local management practices it is necessary to understand the relative importance of local habitat quality and the landscape context. Numerous studies have investigated this in agricultural landscapes, and they often conclude that the landscape context is equally important as local conditions for species diversity and local communities (Thies & Tscharntke, 1999; Weibull et al. 2000; Rundlöf & Smith, 2006).

Another reason for a landscape perspective in biodiversity conservation is that the quality of the matrix between habitat patches may influence dispersal among patches (Vandermeer & Perfecto, 2007). The quality of the matrix is particularly important in areas where most native habitat has already been converted through, e.g., agriculture (Vandermeer & Perfecto, 2007) or urban development.

For the conservation of biodiversity on a landscape or a regional scale it is important to know the distribution of species diversity across spatial scales (Gering et al., 2003). A useful tool for describing this distribution is through partitioning the overall species diversity (gamma) across multiple spatial scales into within-habitat (alpha) diversity and between-habitat (beta) diversity (Lande, 1996; Wagner et al., 2000; Gering et al., 2003). For example, a high beta-diversity, i.e. species turn-over, among sites, indicates that individual sites contribute differently or with different species to the regional species pool. Thus it will not be enough to preserve one or a few sites to preserve the regional species diversity.

Urban-rural gradients

Since the concept of urban-rural gradients was first introduced by McDonnell and Pickett in 1990 it has been a common approach to study the ecological effects of urbanization. Still there is no comprehensive definition of what urban is (McIntyre et al., 2000), or what rural is for that matter (Theobald, 2004). A multitude of ways to describe degree of human modification has been used: subjectively, using transects or mapping land cover, population density, housing/building density and road density (reviewed in Theobald, 2004). Often the descriptions of urbanization have been one-dimensional using only physical measures of the landscape to describe the gradient, while neglecting characteristics of the human population inhabiting the area (Kinzig et al., 2005). Gradients of urbanization are complex, e.g., Dow (2000) highlighted that alone physical measures like percentage of impervious surface, i.e., hard made ground, do not offer a connection to the driving forces behind change in urban areas. For these reasons, in addition to the one-dimensional gradient of urbanization used in *Paper III*, we also examined the relationship among a number of different variables to describe the urban-rural gradient of Stockholm in *Paper I*.

Aims

The main idea behind my thesis was to study the effect of increasing urbanization on different organism groups with important ecological functions. I was also interested in separating the effect of landscape change, local habitat quality and management on species richness, composition and abundance. I also wanted to include the perspective of the people who actually perform the management of green areas and are contributors to the quality of urban green areas as habitat for other species.

The main specific questions addressed by each paper were:

Paper I

- Which measures or combinations of measures of urbanization capture Stockholm's rural-urban gradient, and how do different variables measuring urbanization covary?
- What are the patterns of bird species composition and richness in relation to these urbanization variables?

Paper II

- How do different management practices in three different types of urban green areas (allotment gardens, cemeteries and city parks) affect species richness and abundance of birds and bumble bees?
- How are differences in management practices linked to the local social-ecological context?

Paper III

- How are bumble bee species richness and abundance affected by increasing urbanization?
- What is the relative importance of changes in habitat quality and changes in landscape context for species richness and abundance of bumble bees?

Paper IV

- How are species richness and abundance of trap-nesting insects affected by human land use intensity in an urban and an agricultural landscape context?
- How is species diversity of trap-nesting insects distributed within (alpha) and among (beta) sites, within four different types of landscapes: urban, suburban, rural heterogeneous and rural homogenous?

Interdisciplinary attempts

The aim of urban green areas range from social to ecological, they are meant to fulfill recreational, educational, cultural and ecological needs within the city. Therefore, the understanding of nature and nature conservation within city boundaries is an interdisciplinary and multidisciplinary task (Collins et al., 2000). The methods used in this thesis are derived from different scientific disciplines. I have collaborated with PhD students in different fields and also learnt to practice methods usually applied in the social sciences.

In the summary of this thesis I will present the results from an interview study I did with allotment gardeners. This study is only included in the summary as additional information and does not appear as a separate paper. The attempt of the study was to try to understand what made the allotment gardeners spend so much time and energy on their plots. Further, I wanted to find out how and why they chose to grow the plants they did and if they felt that their allotment garden was threatened by exploitation of some kind.

Material and methods

Description of study area

The field studies were mainly located in Stockholm County, Sweden (Figure 1). This is one of the most densely populated areas in Sweden, with approximately 1.9 million inhabitants (SCB 2007). In *Paper IV* agricultural areas north of Stockholm in Uppsala County were also included. Stockholm is the capital of, and the largest city in Sweden. It is situated on the eastern coast, 59º20'N latitude and 18º05'E longitude, and borders the Baltic Sea. It is characterized by the many waterways that runs through the core of the city and by a relatively high proportion of green areas. Green areas within Stockholm are more or less connected with green areas of the surrounding landscape through a number of green wedges that point towards the centre of the city (Bolund & Hunhammar, 1999). These green wedges are recognized by the municipality of Stockholm as important biological dispersal routes and are the main focus of the green plan of the city (Stadsbyggnadskontoret, 1999). The northernmost surroundings of Stockholm mainly consist of a mixture of suburban areas, mixed coniferous and deciduous forest and agricultural land.

Description of study sites

Different types of green areas were used as study sites: allotment gardens (*Paper II, III*), cemeteries (*Paper II, IV*) and city parks (*Paper II, IV*). Allotment gardens are areas reserved for cultivation of, e.g., vegetables and flowers. They can be found both in central Stockholm and in a more rural setting, but they are always situated in association with human settlement. Local allotment associations rent the land from the municipality for a period of time. This period may differ depending on type of allotment garden and where it is situated, for example gardens with houses are often rented for 25 years whereas gardens with only cultivation and no houses may be rented for only 1-2 years at a time. The allotment gardens are divided into small plots which are leased to inhabitants of the municipality and are managed on a voluntary basis. The areas are rich in flowering herbs, fruit trees and different sorts of vegetables. Cemeteries are like allotment gardens found both in central Stockholm and in more rural areas. In rural areas they can be found in isolation from other human settlements. City parks are, as the name indicates, only found within the city. Cemeteries and city parks are often sparse in flowering herbs, with short-cut grass, tall deciduous trees and small plantations on the graves or in flower beds. Both cemeteries and city parks are managed by one or a few salaried managers.

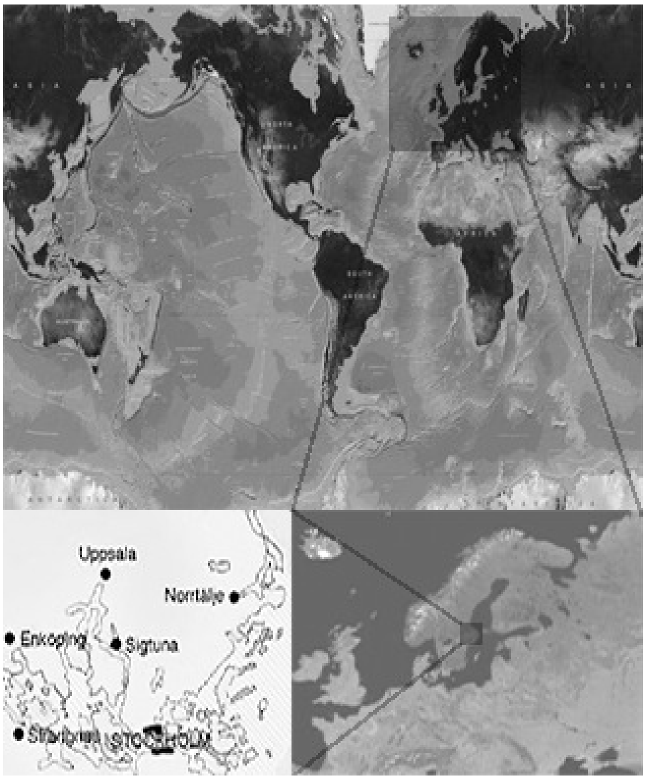

Figure 1. Study area.

Study designs

Paper I

The aim of this study was to describe the gradient of urbanization in Stockholm, using a number of different variables including landscape metrics, physical measures of the landscape and demographic variables. We were also interested in how those variables covary. Another aim was to test the ecological relevance of the gradient, using a data set on species richness and abundance of birds. We gathered information on 20 variables for 116 sample points within two transects running north-south and east-west through central Stockholm. Most of the variables chosen have previously been used in the literature as measures of urbanization (Hahs & McDonnell, 2006), but we also included some variables that we found informative when defining a rural-urban gradient in general and in the context of Stockholm in particular. To reveal the association among the measured variables of urbanization and to identify representative variables we used Principal Components Analysis (PCA). To test the ecological relevance of the variables measured we did a Canonical Correspondence Analysis (CCA) with the set of bird data as response (or species) variable and our measures of urbanization as descriptive (or environmental) variables. For details on the methods used see *Paper I.*

Paper II

In *Paper II* we compared three different types of green areas, allotment gardens, cemeteries and city parks. Here we were interested in how local management of urban green areas affects species richness and abundance of birds and bumble bees, and in trying to understand the management practices from the perspective of the manager. Birds and bumble bees were surveyed in four cemeteries, four city parks and four allotment gardens within Stockholm. To get measures on the quality of the urban green areas as foraging sites for bumble bees, we also did plant inventories in the areas. Information on management practices was derived through interviews with managers of the green areas. These interviews were performed by one of the co-authors on that paper, Stephan Barthel. Therefore I will not describe the interview method further here, but see *Paper II* for details.

Paper III

In *Paper III* we studied bumble bees in 16 allotment gardens along an urban-periurban gradient, with the aim of separating the importance of local and landscape effects on diversity and abundance. Here we chose the physical landscape variable, percentage impervious surface within a defined radius from the studied sites, to describe urbanization. Impervious surface includes all built up area, i.e. buildings, roads, railroads, industrial areas. We gathered information on the percentage of other land-cover types as well: arable land, forest and other green areas (i.e. pastures, gardens, city parks). The total length of boundaries between different types of land-cover was also measured as especially forest boundaries and field margins are known to be important both for nest searching and foraging bumble bees (e.g., Svensson, et al. 2000; Kells et al., 2001). We also gathered information on the quality of the allotment gardens as foraging sites for bumble bees, by doing inventories of flowering plants in the allotments.

Paper IV

In *Paper IV* we wanted to compare trap-nest communities in agricultural and urban landscapes, differing in land use intensity. Here we wanted to standardize the local habitat by using study sites that were similar in appearance and management. We had 29 study sites; 25 cemeteries and 4 city parks, within urban and agricultural landscapes. The agricultural landscape was divided into two groups: rural homogeneous (7 sites) and rural heterogeneous (9 sites), based on the Simpson diversity of landscape elements within 1000 m of the studied sites. The urban landscape on the other hand was divided into two groups: suburban (5 sites) and urban (8 sites), based on the percentage impervious surface within 1000 m radius from the studied sites.

Study organisms

The focal organisms of my studies were bumble bees (*Paper II, III*), trap-nesting bees and wasps and their natural enemies (*Paper IV*) and birds (*Paper I, II*). Bumble bees were chosen as they are important as pollinators of many flowering plant species (Corbet et al., 1991), relatively well studied and easy to monitor (Benton, 2006) and known to most people. Wild bees, including bumble bees, play an integral role as pollinators of both wild plant species and crops (Corbet et al., 1991; Klein et al., 2007). Trap-nesting bees and wasps and their natural enemies is here used as a generic term to describe the insects that nest in artificial reed trap-nests. They were chosen as study organisms as they have previously been suggested as suitable bioindicators of habitat quality and environmental change (Tscharntke et al., 1998). They may also have important functions as pollinators and as natural enemies of herbivorous pest insects such as aphids, caterpillars and leaf-beetle larvae and they readily nest in artificial trap-nests (Tscharntke et al., 1998). Birds were chosen as study organisms for *Paper I* and *II* because they have important ecological functions for seed dispersal (e.g., Robinson and Handel; 1993, Sekercioglu et al., 2004) and pest regulation (e.g., Sekercioglu et al., 2004). They are, like bumble bees, recognized by the managers of urban green areas and other people living in the city, and among the most well studied organism groups in urban areas (e.g., Andersson, 2007).

I have surveyed bumble bees and trap-nesting bees, wasps and their natural enemies, while the studies of birds were performed by my co-author on *Paper I* and *II*, Erik Andersson, therefore I will not give detailed information on birds. Below I will try to give a more thorough description of my study organisms and their situation in human dominated landscapes. I will also shortly describe the methods I have used to survey them. For details on methods used to survey birds see *Paper I* and *II*.

Bumble bee life cycle

I will give a short description of the general life cycle of bumble bees following that given in Goulson (2003). Bumble bees (*Bombus*) are social insects with a queen, workers and males. They generally have an annual life cycle. In the spring over-wintered queens emerge and start searching for a suitable nesting site. The choice of nesting sites varies between species, some species always nest below ground in pre-existing holes, and others just above ground in, e.g., tussock of grass and still others use a variety of nest sites both above and below ground, e.g, old birds' nests or artificial cavities. When the queen has found a suitable nesting site she provisions it with pollen and lays her first eggs that will develop into bumble bee workers. The bumble bee larvae need to be provided with pollen and nectar to grow. After about 10-14 days the larvae pupate and after another 14 days the pupea hatch. As the first bumble bee workers emerge they take over the collection of pollen and nectar for their younger siblings, while the queen stays in the nest to lay eggs. By the end of the summer or when the colony has reached a sufficient size (which varies between species) new queens and males are reared. The males emerge and start to fly certain routes to find a mate. Before the winter all bumble bees die except for the new queens that have been mated and over-winters to the next spring.

Bumble bees in human dominated landscapes

As mentioned above the bumble bees are dependent on pollen and nectar for their survival and reproduction. They also need suitable nesting sites and the queen needs a protected place to over-winter. Bumble bees are called central place foragers as they need to return to their nest to unload their collected pollen. Therefore their nest has to be situated within flight distance from foraging sites. They also need a continuous availability of suitable flowering plant species to be able to build up a colony. During the last decades several bumble bee species have declined and become locally extinct, both in Europe and North America (Goulson, 2003). Land use conversion and loss of flower resources and natural habitats due to changed agricultural practices is likely the main reason for this decline, whereas the effect of urbanization is less investigated (Goulson, 2003; Benton, 2006). Interestingly, some bumble bee species are still widespread and common (Goulson et al., 2005; Benton, 2006). The reason for this difference in response to changes in human land use is not clear but has been attributed to species specific traits such as tongue length (Goulson et al., 2005), diet (Goulson et al., 2004) species' geographical ranges (Williams, 2005), emergence time (Fitzpatrick et al., 2007) and foraging distance (Benton, 2006). Differences in foraging distances have been explained by differences in body (Westphal et al., 2006; Greenleaf et al., 2007) and colony size (Westphal et al., 2006).

Bumble bees have mainly been studied in the agricultural landscape and only a few studies have addressed the effect of urbanization on wild bee communities, including a few species of bumble bees. In general these studies have found that urban green areas can harbour a large number of bee species (Saure, 1996; Frankie et al., 2005), but that they are less diverse than wilder areas in the surroundings of the city (e.g., McIntyre & Hostetler, 2001; Eremeeva & Sushchev, 2005; Tommasi et al., 2005; Matteson et al., 2008). For example Tommasi et al. (2004) recorded 56 bee species, of which 6 were bumble bees, in the city of Vancouver. Bee abundances were higher in botanical and community gardens, with high flower abundances, but bee diversity was higher in wild areas. In community gardens in New York City, 54 bee species (i.e., 13% of the recorded New York State bee fauna) were observed, of which 5 species were bumble bees (Matteson et al., 2008). The bee fauna of community gardens was more dominated by cavity nesting and exotic species in comparison to that of surrounding wild habitats. McFrederick and LeBuhn (2006) found that urban parks in San Francisco were as diverse and had higher abundances of bumble bees than nearby larger wild parks. However, they recorded only four bumble bee species within the city and the city parks were strongly dominated by one common species *Bombus vosnesenskii*. Urban habitats have previously been found to support large populations of two common bumble bee species *B. pascuorum* and *B. terrestris* (Chapman et al., 2003). Most of the urban studies of wild bees have addressed the suitability of urban green areas as habitat for bees and have not separated the effect of landscape changes due to urbanization from the effect of changes in habitat quality.

Bumble bee surveys

Daylight (9.00 AM to 19.00 PM) surveys of bumble bees were done in good weather (temperature >15°C, sunny or scattered clouds). Each site was visited several times during the summer (June to August) in varying order so that all sites were surveyed both in the morning and in the afternoon. At each site, point observations of bumble bees were conducted in study plots, consisting of a quadrat (*Paper II*) or a triangle (*Paper III*) with sides three meters. The number of plots depended on the size of the site and was related to the logarithm of the area. The plots were evenly distributed within the allotment gardens, cemeteries or city parks and placed to contain plant species in flower. All bumble bees entering the study plot during a five minute survey period were identified to species according to Løken (1973) and the plant species visited were recorded. When species determination was not possible by sight, individuals were caught with a net and either determined to species on site or brought to the laboratory for later determination. The five minutes were measured with a stopwatch that was temporarily stopped while catching a bumble bee.

Trap-nesting bees and wasps

Trap-nests are colonized by bees and wasps (Hymenoptera: Apidae, Sphecidae, Eumenidae, Pompilidae) that naturally build their nests in above ground holes in dead wood or grass stems (Tscharntke et al., 1998). They lay eggs in cells and depending on species they provide each cell with pollen, leaf beetle larvae, aphids, caterpillars or spiders as food for their larvae (Tscharntke et al., 1998; Budriené, 2003). The adults forage on flowers for pollen or nectar. Thus besides suitable nesting sites the bees and wasps also need food resources as pollen nectar and insect prey (Tscharntke et al., 1998). Natural enemies of the bees and wasps also colonize the trap-nests if their host species are present.

Trap-nests have mainly been used to study bees and wasps and their natural enemies in the agricultural landscape in different parts of the world (e.g., Tscharntke et al. 1998; Steffan-Dewenter, 2003; Tylianakis et al., 2005, Klein et al. 2006, Sjödin, 2007). In an agroforestry system in Indonesia, Klein et al. (2006) found that the number of species of trap-nesting insects was negatively related to distance to forest. In another study Steffan-Dewenter (2002) found that the total species number of bees and wasps increased significantly with an increasing proportion of semi-natural habitats within a radius of 250 m, 500 m, and 750 m. The pattern was determined mainly by the increasing number of wasp species in landscapes with higher proportions of semi-natural habitats. One bee species, *Osmia rufa*, inhabiting trap-nests, was found to be most limited by nesting sites (Steffan-Dewenter & Schiele, in press). Sjödin (2007) found that reproductive success of trap-nesting bees in semi-natural grasslands in Sweden was related to presence of buildings within the agricultural landscape. This indicated that presences of farmers and structures related to farmsteads were important for these species.

Trap nests

The trap-nests consisted of PVC tubes with a length of 20 cm and a diameter of 10 cm, filled with 20 cm cuts of reed, *Phragmites australis* (see Figure 2). Within each trap-nest there were 150-200 straws of reed. At each site six trap-nests were placed 1-1.5 m above ground on two fence posts (three trap-nests on each). The PVC tubes were open at both ends. A wooden plate was placed on top of each post to protect the trap-nests from rain. Trap-nests were put out in spring (late April) and recollected in the autumn (mid-October) the same year. The trap-nests were over-wintered outdoors under roof until mid-February, when they were taken inside a green-house with a constant temperature of 20°C. The six trap-nests from each site were put into a hatching-box with a small hole at the front where a glass tube was placed to collect the emerging insects. The tubes were checked and emptied every day until there were no more emerging individuals for at least two weeks. This happened by the end of April.

Figure 2. Trap-nests, without roof.

Interviews

Background and methods

The more I have learnt about ecology in human dominated areas in general and in urban areas in particular, the more convinced I have become of the importance of recognizing the human perspective. Urbanization is both an ecological and social phenomenon, thus it is an interdisciplinary field (McIntyre et al., 2000), and requires an interdisciplinary approach to be understood. Several authors have recognized that the study of urban ecosystems requires integration of natural and social sciences (Pickett et al., 1997; Niemelä, 1999; Alberti et al., 2003) and that each discipline would be strengthened if it were to include variables usually attributed to the other (McIntyre et al., 2000). For *Paper II* I was collaborating with two other PhD students. One of them did interviews with managers to compare the management practices of three different types of green areas to understand what lies behind differences in management practices. My main studies of bumble bees in urban green areas were conducted in allotment gardens. From this I came in contact with allotment gardeners and became interested in developing my studies by doing interviews with the gardeners. I was fascinated by the time and energy they spent on their plots and wanted to understand what drove them to do so. As I knew that bumble bee abundance and species composition was affected by the plants grown within the allotment gardens (*Paper III*), I was also interested to know what influenced the gardeners' choice of plants. As allotment gardens are generally disregarded by planning authorities (*Paper II*), I was interested to know if the allotment gardeners felt that their allotment was threatened by exploitation.

To choose people to interview I went to four of my allotment gardens, situated at different places along the periurban to urban gradient defined in *Paper III*. I asked people that I met if they were interested to participate in an interview about being an allotment gardener. If they were interested we booked a date for the interview. All allotment gardeners interviewed were people that spend a lot of time on their plots. I did a total of ten interviews, which is a reasonable number for a qualitative interview study (Kvale, 1997). The interviewed allotment gardeners knew who I was before the interviews, as I had surveyed bumble bees in the allotments during several years prior to the interviews. They also knew of my background as an ecologist and of my interest in bumble bees, which may have influenced some of their answers to my questions. I had been speaking to several allotment gardeners during my bumble bee surveys, so that I had an idea about which questions would be interesting and relevant to ask, when I designed the interview study.

Because I mainly was interested in what motivates the allotment gardeners to manage their plots, I chose a qualitative interview method rather than a quantitative one. The qualitative method focuses on the ideas and the perspective of the interviewee, while the quantitative method focus on the researchers interest (Bryman, 2001). In qualitative interviews it is desirable to let the interview move in different directions, because this will result in knowledge about what the interviewee experiences as relevant and important (Bryman, 2001). The qualitative interview allows the researcher to ask new questions to follow up an interesting answer (Kvale, 1997, Bryman, 2001). Thus the questions asked will differ between interviews to some extent depending on the answers given. My interviews were semi-structured (Bryman, 2001), as I had some specific questions or themes that I wanted to discuss. This means that I had a number of questions written down, but I did not always ask them in the same order and I could ask follow up questions when I felt this was needed. Before I started the interview I explained how it would be structured and in what context I would use the answers. I also said that it should not be possible to link a specific statement to a certain person. Therefore the respondents will remain anonymous in this text. All interviews were recorded and later transcribed. Then statements relevant to the subjects discussed here were identified from the transcriptions.

I do not aim at giving a comprehensive picture of what allotment gardeners in general think, but rather let some of the gardeners I have met during the years speak their mind and give their perspective on what allotment gardening is about. The qualitative interview study is a case study and the people that are interviewed in a qualitative study cannot be representative for a whole population (Bryman, 2001). Instead through the interpretation of the interviewees' statements I can start to build a theory about what drives the allotment gardeners to put so much time and effort into their plots.

Findings of the interview study

Background – the allotment movement

First, I would like to give a background to what an allotment garden is and what the idea behind the allotment movement was from the beginning. To give you a more lively description of the history of allotments in Stockholm I will borrow the voice of one of my respondents to tell you the story as it was told to me:

> This area is an old allotment garden, in 1917 it became an allotment association, and it will become 90 years next year. It was this, the 1st World War, one could say. In Stockholm they started to found allotment gardens in 1905, rather late, in Denmark they already had 40 000 allotments at that time. Well, it came from Germany, the idea of allotment gardens for poor workers, open-air places so they would become better workers, but also get a better life, also for the children who at that time died very young.
>
> Eventually it came to Stockholm and the first area was established at Djurgården, Söderbrunn, it is still there and two other areas on Söder, Barnängen and Eriksdalslunden in 1906, they will celebrate 100 years this year. After that a lot of areas were established, but then this 1st World War came on, and there was a famine in Stockholm one could say. There were hunger riots here on Söder. People thought that the businessmen were hiding goods to be able to sell them much more expensively to those who could afford. Then the government decided that they would provide land, which was not in use, for cultivation. Even the city parks, Humlegården and Kungsträdgården, were ploughed up. They distributed seed potatoes to people, and some people ate them directly of course. That was in 1917 and the yield of potatoes in Stockholm was 870 000 kg, which was exceptional! It was harsh times so they had guards to protect the potatoes from thieves. This area is such an old potato field. It is steep and slopes abruptly down to the water. People worked hard to even out the ground, but if you look at a plan

> over the area the plots are terribly irregular. Then gradually they started to build small houses on the plots, for shelter. They were probably not allowed to do that, but the city thought that this area was so far from the centre so they agreed to the formation of an association here in 1917. At that time the allotment garden went all the way down to the water, but then in the 30's the hospital, Södersjukhuset, was built and in connection to that the railway. Then all the allotment gardeners here were noticed to leave, but some of them clung to the hill and this association still remains, which is nice.
>
> Then during the 40's and 50's it was bad times for allotments, it was considered a sign of poverty to have an allotment. In the 60's there was a housing shortage and allotment gardeners let people rent their small houses, which had no water or electricity. The allotment gardeners only had one year contracts so they did not care to improve their houses. But when that terrible thing happened in 1965 in Dalen, where a large allotment area with 400 plots was burnt down and destroyed, all allotment gardeners went crazy. They united and put a pressure on the authorities, which led to a real improvement of the standard. We got 25 year contracts and people started to invest in their plots and their houses. (Respondent 1)

The purpose of allotment gardens has changed a lot during the last hundred years. In the beginning of the 20^{th} century, and also during the World War II, the allotment gardens were mainly used to grow potatoes and vegetables for the survival of inhabitants of the city, whereas today allotment gardens are mainly used for recreation by the citizens. However, already when the allotment movement came to Sweden, much thanks to the work of one woman, Anna Lindhagen, there was an idea of the social-aesthetic value of allotment gardens (Barthel et al., 2005; http://www.koloni.org/pdf/01.pdf).

The importance of the allotment garden

In *Paper II* we found that the local ecological knowledge and the sense of place were much more pronounced among allotment gardeners than among managers of cemeteries and city parks, and that both local ecological knowledge and sense of place influenced the management practices. The term local ecological knowledge was used in *Paper II* as the knowledge held by an individual or a specific group of people about their local ecosystem. Sense of place is an intimate emotional attachment to a place, created through firsthand interaction between humans and places (Kaltenborn, 1998; Cantrill & Senacha, 2001). However, local ecological knowledge and sense of place cannot be considered the only social drivers of the management of allotment gardens. Through my interviews with gardeners I found that what made the respondents spending the many hours and the energy in their gardens, was that doing this felt meaningful and made them feel good.

> …it [the allotment garden] gives you peace in the soul for the rest of the life in a way… the allotment garden is peace, harmony, close to nature, here you can be as you like. (Respondent 8)

For many of them being an allotment gardener had become an important part of their life and identity, almost a lifestyle.

> …it became a way to survive for me. You know I don't even know if I would have stayed in Stockholm if this [get an allotment garden] had not happened, actually. (Respondent 2)

Both their local ecological knowledge and the sense of place, which increase and develop with time spent managing and interacting with the garden, have certainly contributed to this. However, also the more immediate experience of well-being that occurs when being out in nature and doing something with your hands and to see how it grows as a result of your work, are important drivers for the gardeners.

> But it is the work, one say work but it really isn't, that I like. I can't stop, I am digging and taking care of the plants all the time. (Respondent 3)

> I like to see when it grows and it is fun to work with your hands. It is a way to clear your mind, when you are standing here, you relax somehow. (Respondent 5)

Choice of plants

The reasons varied to why the allotment gardeners in my survey grew the plants they did. All of them grew both vegetables and flowering plants and many of them also had fruit trees and raspberry and currant bushes. Some of the plants were gifts from others; friends or relatives. Many of them kept plants that had once grown in their parents or someone else's garden, as memories of the people or the garden. They also shared plants with each other within the allotment garden. If someone was tired of a plant he or she could give it to someone else within the area. Most of them had a variety of different flowering plant species. However, they often seemed to have a favourite species that they always wanted to have, either because it was beautiful to look at or because of its scent. Moreover, they grew plants that they had learnt grew well in their garden. Only one respondent said that she thought about the bees and bumble bees, therefore she kept the *Impatiens glandulifera*. However, most of them had observed which plants were most visited by bumble bees and other bees.

Threats to the allotment garden

Most of the gardeners in this survey did not feel a direct threat of exploitation against their allotment garden, for various reasons. One of the gardens was directly protected as a national interest (Riksintresse). Another garden was situated within the Stockholm National Urban Park (http://www.nationalstadsparken.org/bok/summary.pdf, Borgström et al., 2006) and therefore the gardeners felt that the area was indirectly protected. A third garden lay close to a nature conservation area and the gardeners thought that this might give it protection. Moreover, most of the gardens were placed on land that was difficult to build upon. The respondents with plots in gardens that were used for cultivation only (without proper houses and with a short contract, a few months to 2 years), felt somewhat more threatened than those with long contracts. None of the respondents felt a direct threat to their gardens, but they did not feel sure about what kind of decisions the authorities would make in the future. Some of them thought that having houses on their plots increased the protection against exploitation. Further, many respondents emphasized the importance of the area being open to the public as a means for stronger protection.

> Yes, that is what I believe… because I mean it should not be a small privileged group that is allowed to be here and no one else. The more people that are allowed in here the more people will be interested in how it looks and in preserving it, I think. (Respondent 7)

Results

Describing the urban-rural gradient

Two main ordination axes were revealed in the PCA of our 20 measures of urbanization. The variables associated with the first axis were mainly landscape metrics such as, largest patch index (LPI), landscape shape index (LSI) and fractal dimensions, and variables associated with the second axis were demographic variables as well as the proportion impervious surface and coniferous forest (Figure 3). This indicates that the gradient of urbanization in Stockholm could be simplified to one surrogate variable for the landscape metrics and one demographic variable or proportion impervious surface.

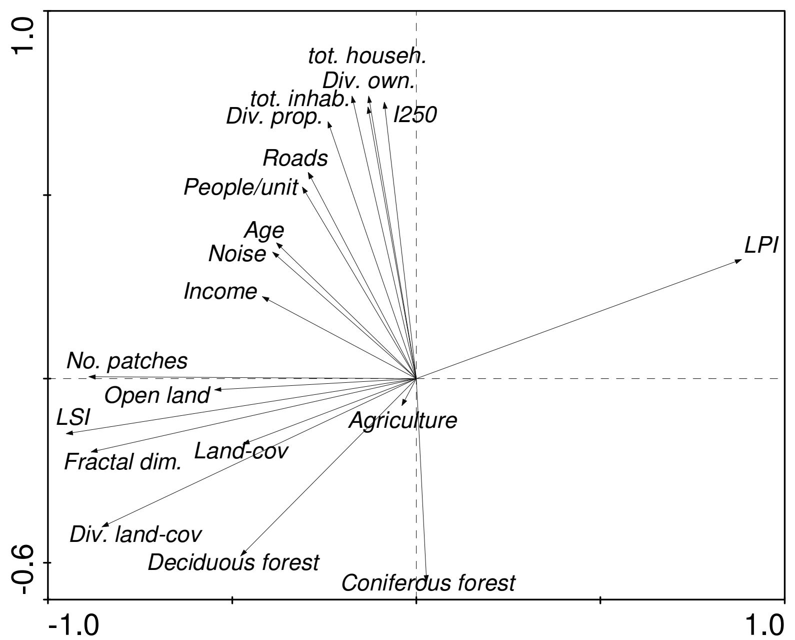

Figure 3. PCA with 20 measurements of urbanization within 250×250 m cells. The first two axes explain 50.5% of the variation in the data. I250= Percentage impervious surface within 250 m cells, LPI=Largest Patch Index, Div. own.=Simpson's diversity of land owners, Tot. househ.=Total number of households, Tot. inhab.=Total number of inhabitants, Div. prop.=Simpson's diversity of properties, Roads=Road network density, People/unit=People per unit impervious surface, Age=Age of development, Noise=Acoustic environment, Income=Mean income (per household), No. patches=Number of patches, Open land=Percentage open land, LSI=Landscape Shape Index, Fractal dim.=Fractal dimensions, Land-cov=Land-cover richness, Div. land-cov=Simpson's diversity of land-cover, Deciduous forest=Percentage deciduous forest, Agriculture=Percentage agricultural land, Coniferous forest=Percentage coniferous forest. See *Paper I* for explanations of the variables.

In the CCA with measurements of bird species data as species variables and the measures of urbanization as environmental variables, the bird species were mainly associated with one of four sets of measures of urbanization: i) percentage coniferous forest, ii) percentage deciduous forest, iii) percentage impervious surface, owner diversity and number of inhabitants, iv) number of patches (Figure 4).

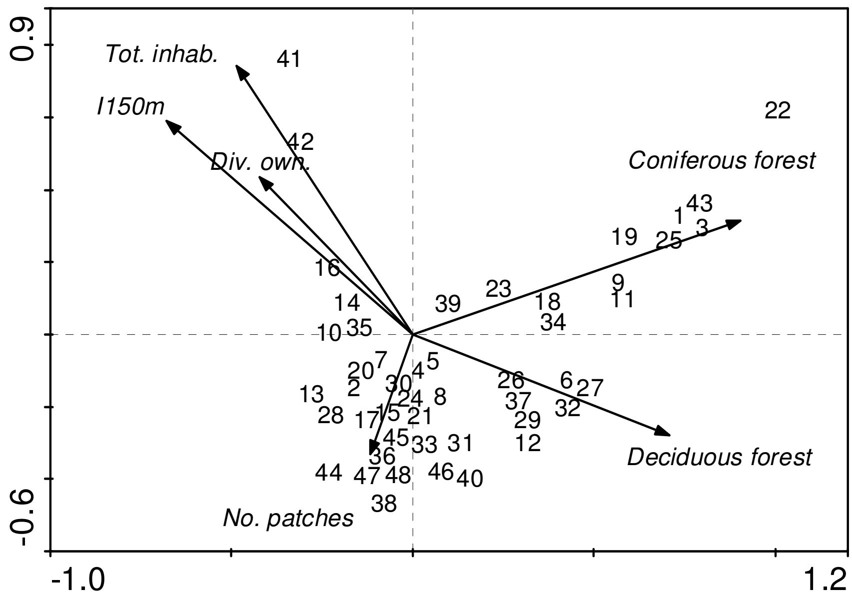

Figure 4. Result of CCA with bird species and measurements of urbanization within 150 m radius. The variables shown in the figure significantly explained 20.4% of the variation in bird species data (sum of all canonical eigenvalues: 0.752, sum of all eigenvalues: 3.692, 0.752/3.692=0.204 i. e. 20.4%). 1=*Turdus iliacus*, 2=*Turdus pilaris*, 3=*Turdus philomelos*, 4=*Turdus merula*, 5=*Parus major*, 6=*Parus ater*, 7=*Parus caeruleus*, 8=*Sitta europea*, 9=*Certhia familiaris*, 10=*Pica pica*, 11=*Garrulus glandarius*, 12=*Corvus corax*, 13=*Corvus monedula*, 14=*Corvus corone*, 15=*Sturnus vulgaris*, 16=*Passer domesticus*, 17=*Passer montanus*, 18=*Fringilla coelebs*, 19=*Carduelis spinus*, 20=*Carduelis chloris*, 21=*Carduelis carduelis*, 22=*Pyrrhula pyrrhula*, 23=*Coccothrautes coccothrautes*, 24=*Ficedula hypoleuca*, 25=*Regulus regulus*, 26=*Phylloscopus trochilus*, 27=*Phylloscopus sibilatrix*, 28=*Sylvia communis*, 29=*Sylvia atricapilla*, 30=*Sylvia curruca*, 31=*Sylvia borin*, 32=*Acrocephalus scirpaceus*, 33=*Phoenicurus phoenicurus*, 34=*Erithacus rubecula*, 35=*Motacilla alba*, 36=*Anthus trivialis*, 37=*Dendrocopos major*, 38=*Phasianus colchicus*, 39=*Columba palumbus*, 40=*Columba oenas*, 41=*Columba livia*, 42=*Streptopelia decaocto*, 43=*Troglodytes troglodytes*, 44=*Alauda arvensis*, 45=*Emberiza citrinella*, 46=*Luscinia luscinia*, 47=*Saxicola ruberta*, 48=*Carpodacus erythrinus*.

Effects of urbanization and landscape context

A general result of my studies was that species diversity decreased with increasing urbanization, quantified by percentage impervious surface within the landscape (*Paper I*, *III*, *IV*). Both bird (*Paper I*) and bumble bee (*Paper III*, Figure 5) species richness significantly decreased with increasing percentage impervious surface within the surrounding landscape. Bird species composition, on the other hand, was related to the percentage of different forest classes, deciduous and coniferous forest, within the surrounding landscape (*Paper I*). There was a higher variability in bumble bee visits to individual plants, especially for long-tongued and small bumble bee species, in urban allotment gardens than in allotment gardens in a more rural context (*Paper III*). Still, also the most urban sites had a rather high number of bumble bee species. The five most urban sites had 11 species together (*Paper III*).

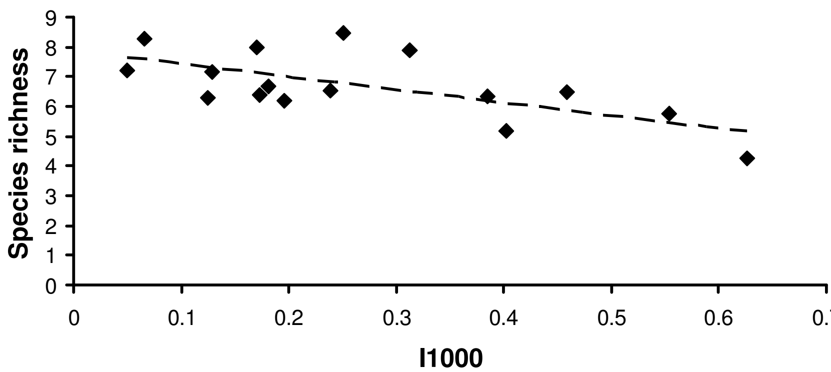

Figure 5. The relationship between bumble bee diversity (number of species after rarefaction to 25 individuals) and the proportion of impervious surface within 1000 m radius (linear regression: p=0.008, R^2=36.7%).

The within-site (alpha) species richness of trap-nesting insects was lower in the urban landscape than in any of the rural landscape types (*Paper IV*, Figure 6). The number of species found in the urban landscape was low and in three of the urban and one of the suburban sites no insects colonized the trap-nests (*Paper IV*). Also, the abundance of trap-nesting insects tended to be lower in urban than in suburban and any of the rural landscapes (*Paper IV*). The rural heterogeneous landscape contributed with most unique species, and most of the species found in urban or suburban sites were also found in rural sites. The trap-nest occupation was highly variable in all landscape types, which resulted in high beta species richness among sites within landscapes (*Paper IV*).

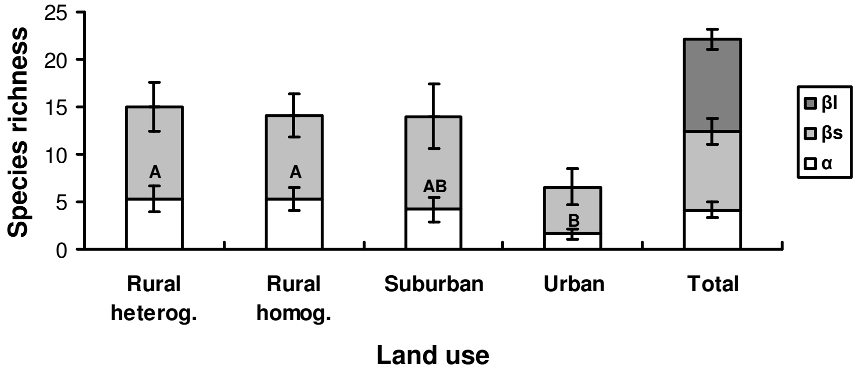

Figure 6. Additive partitioning of the species richness of trap-nesting insects. Species richness within each landscape type was divided into within site (α) species richness and among site (β_s) species richness. For the total species richness the species turn-over (β) was divided into among landscape (β_l) species richness and among sites (β_s) species richness. Error bars show the standard deviation. Different letters indicate significant differences in alpha species richness.

Effects of habitat quality and management

Bumble bee abundance was much higher in flower rich allotment gardens than in cemeteries and city parks, which indicates that the management practices of different types of urban green areas is important for bumble bees (Figure 7, *Paper II*). Also the management of the allotment gardens themselves seemed to be relevant both for abundance and species composition of bumble bees (*Paper III*). Bumble bee abundance significantly increased with flower abundance within allotment gardens, while bumble bee species composition was related to the type of allotment and species richness of flowering plants. Most species increased with increasing flower richness and were more common in allotment gardens with cultivated plots only and no houses. The plant families that were most influential on bumble bee species composition were Lamiaceae and Fabaceae. This suggests that the type of allotment garden and the choices and decision of individual allotment gardeners is not negligible.

Birds also seemed to be influenced by management practices in different types of green areas (*Paper II*). The community structure and the species composition of birds differed between the different types of green areas. The relative abundance of both seed dispersers and insectivores differed between allotment gardens and city parks, and the species composition of insectivores differed between allotment gardens and cemeteries.

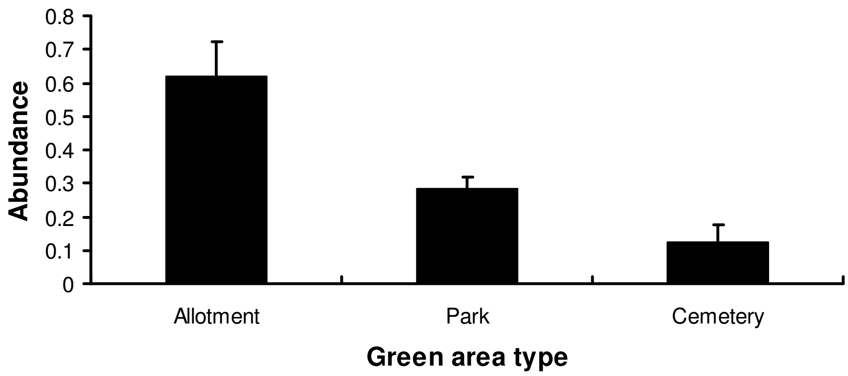

Figure 7. The mean number of bumble bees observed in a study plot in 10 minutes. differed significantly between the three different types of green areas (one-way ANOVA: F=13.57, p=0.002). The error bars show the standard error of the mean.

Together these results indicates that the management practices of urban green areas are relevant for species performing important ecosystem services as pollination, seed dispersal and pest regulation, within the city. The management practices of different urban green areas in turn were affected by the social organization of the managers, and by the managers' local ecological knowledge and sense of place (*Paper II*). Both local ecological knowledge and sense of place were more pronounced among allotment gardeners than among managers of cemeteries and city parks.

Discussion

A general result of the studies presented in this thesis was that species richness decreased with increasing urbanization, quantified by the percentage of impervious surface within the surrounding landscape (*Paper I*: birds, *Paper III*: bumble bees, *Paper IV*: trap-nesting insects). Increasing percentage of impervious surface also represented decreasing amounts of natural habitats such as, percentage deciduous and coniferous forest (*Paper I*) and potential nesting sites such as length of forest, field and pasture boundaries (*Paper III*). Decreasing percentages of suitable habitats within a certain radius indicate smaller habitat patches and increasing distances to other suitable habitats within the landscape. Connectivity among habitats has been suggested as important for the ability of urban green areas to support biodiversity (e.g., Niemelä, 1999; Melles et al., 2003; Elmqvist et al., 2004).

Impervious surface has previously been used as a measure of urbanization and seemed to be a reasonable measure for the urban-rural gradient in Stockholm, studied in *Paper I*. Percentage impervious surface was positively correlated with several demographic variables, for example, population density, diversity of owners, and number of households. This will probably be the case also in other cities. Our measures of urbanization were mainly ordered along two axes, one represented by landscape metrics and the other by demographic variables, but also percentage impervious surface and coniferous forest (*Paper I*). This indicates that the urban-rural gradient in Stockholm could be simplified to two surrogate variables one demographic variable (or impervious surface) and one landscape metrics. A similar pattern with two distinct gradients among a number of measures of urbanization was also found in Melbourne (Hahs & McDonnell, 2006), but their gradients were represented by different variables than in our study. However, for most bird species the percentage deciduous and coniferous forest within the landscape was more relevant than impervious surface (*Paper I*).

The percentages of deciduous and coniferous forest within the landscape at 150 m radius were the best predictors of two sets of bird species (*Paper I*). In *Paper II* both species composition and relative abundance of birds differed between the three types of green areas. These results imply that having different types of green areas within the city increases the total number of bird species. Species composition of bumble bees was also most influenced by local habitat quality (*Paper III*). Both birds and bumble bees are relatively mobile and can probably find and choose their habitat to a larger extent than less mobile species, which are more prone to show time-lag effects (Löfvenhaft et al., 2004). Similar patterns, where local conditions were the strongest predictor of species composition, have earlier been reported for other mobile organisms (Angold et al., 2006; Small et al., 2006).

Species composition of bumble bees was influenced by species richness of flowering plants, but also by the type of allotment garden (*Paper III*). Many bumble bee species were more common on allotment gardens without houses. Those gardens had often grown wilder than gardens with houses, and they might have provided more nesting sites for bumble bees in, e.g., tussocks of grass (Kells & Goulson, 2003). The plant families that were most influential on bumble bee species composition were Lamiaceae and Fabaceae. Both Lamiaceae and Fabaceae include several plant species known for their attractiveness to bumble bees (Fussell & Corbet, 1992, Goulson et al., 2005; Carvell et al., 2006). *Origanum vulgare* and other aromatic plants like *Nepeta cataria*, *Lavendula angustifolia* and *Salvia* spp., belonging to Lamiaceae, were frequently visited by bumble bees of many species. Also, *Lupinus* spp. (Fabaceae), were often visited by many bumble bee species. *Trifolium pratense*, known as an important source of pollen and nectar especially for long-tongued bumble bee species (Goulson et al., 2005; Carvell et al., 2006), was another species of Fabaceae often found in the allotment gardens.

In my interview study I found that the gardeners' choice of plants mostly depended on other factors than to promote bees. However, all of the respondents grew a variety of different plant species and most of them kept plants readily visited by bumble bees, e.g., aromatic plants. Thus the preference for flowering plants among allotment gardeners and bumble bees often seemed to coincide. Most of the interviewed gardeners also kept fruit trees, strawberries and raspberry bushes and knew that these plants were dependent on pollination for fruit set. Together, the variety of flowering plant species grown in each plot, and the high number of gardeners with different flower preferences within each allotment area, led to an overall high diversity of flowering plants within each site. Bumble bees benefited from high species richness and abundance of flowering plants within allotment gardens (*Paper II, III*), while allotment gardeners benefited from high species richness and abundance of bumble bees.

Bumble bee abundance was most influenced by local habitat characteristics, such as flower richness and abundance (*Paper II, III*), whereas abundance of trap-nesting insects was also influenced by the surrounding landscape (*Paper IV*). Cemeteries and city parks are probably not particularly good as habitats for trap-nesting bees and wasps, given their low abundance of flowering plants. Therefore, the insects found in our trap-nests were probably dependent on food resources provided in the landscape surrounding the sampled sites. The use of different methods means that abundances of bumble bees and of trap-nesting insects reflect different things. Bumble bees were surveyed while foraging, and we have no measures of the reproductive success of bumble bees or the quality of the sites as nesting sites. Nests are founded by a single queen, who is mostly mated once. Therefore the nest density within an area determines the effective population size (Darvill et al., 2004). However, bumble bee abundance primarily indicates the quality of the site as foraging area. Bee abundance has previously been shown to increase with local flower abundance (e.g., Sjödin, 2007). Differences in abundance of trap-nesting insects may both reflect reproductive success and the availability of food-resources for adults and larvae in the different landscapes (Sjödin, 2007, Steffan-Dewenter & Schiele, in press)

In *Paper IV* we found that alpha species richness of trap-nesting insects was lower in sites within an urban landscape than in sites within rural landscapes. This indicates that the trap-nesting insects are negatively affected by urbanization. The number of species found in urban sites was generally low and in three of the urban sites no insects occupied the trap-nests. Trap-nesting bees and wasps are known to have relatively specific habitat requirements both regarding nesting sites and food resources and they need those resources within flight distance (Tscharntke et al., 1998; Budriené, 2003; Sjödin, 2007). They also have relatively short flight distances (Gathmann & Tscharntke, 2002), and may respond to landscape changes at a smaller scale than for example many species of bumble bees (Steffan-Dewenter, 2002; Steffan-Dewenter at al., 2002). Species found in the urban landscape seemed to be a subset of the species found in the rural landscapes. Therefore, for conservation of trap-nesting insects in urban green areas it is important to consider the landscape surrounding the city and the requirements of species present there. Beta species richness was high in all landscapes surveyed (*Paper IV*), which suggest that the qualities determining which species could be supported in the area varied among sites or that the sites were isolated from other suitable habitats (Diekötter et al. 2007; Veech & Crist, 2007). To increase the population of trap-nesting species in these human dominated landscapes it is important both to improve colonization abilities by increasing connectivity among suitable habitats and to improve habitat qualities. Increased connectivity among suitable habitats within the landscape would increase the probability for females to find their way to breeding, nesting and food sources. To improve the local habitat quality one should promote a diversity of trees and bushes of different ages for good nesting abilities (Sjödin, 2007; Steffan-Dewenter, in press) and increase food supply through continuous management for areas with rich supply of flowering plants (Sjödin, 2007).

Together the results of my studies suggest that management both at a local and a landscape scale influences birds, bumble bees and trap-nesting insects in the studied human dominated landscapes. The social drivers of local management of urban green areas found in *Paper II* and in my interviews were local ecological knowledge, sense of place and the well-being experienced while managing the areas, but also a more subtle feeling of meaningfulness. Both local ecological knowledge and sense of place were more pronounced among allotment gardeners than among managers of cemeteries and city parks (*Paper II*). Also, the managers of allotment gardens were more flexible than managers of cemeteries and especially city parks who were more bound to rules and regulations (*Paper II*). This influenced the management practices and measures taken to enhance the quality of the urban green areas for pollinators, seed dispersers and insectivores. Such management practices were more common in allotment gardens than in the two other types of green areas. In allotment gardens there are numerous managers, while in city parks and cemeteries there are only one or a few. In green areas with only one manager the local ecological knowledge risks being lost when that person leaves or retires. Many managers facilitate the maintenance of local ecological knowledge in the area over time. In *Paper II* we argue that the involvement of citizens also in the management of cemeteries and especially city parks would be likely to promote the same positive qualities that were found among managers in allotment gardens.

However, not only the local management, but also the management on a larger scale was important for diversity (*Paper I, III, IV*), but few local managers interviewed held a landscape perspective (*Paper II*). The landscape perspective was, instead, held by the planning authorities. Therefore transfer of knowledge between groups of managers and planners appears to be important to enhance biodiversity planning in urban areas (e.g., Andersson, 2007). Green areas such as allotment gardens and cemeteries are mostly recognized for their recreational, cultural and historical values, while their importance for biodiversity within the city is often overlooked in green plans developed by the municipalities (*Paper II*; Tekniska kontoret Täby, 2005; Markkontoret Stockholm, 2006). Even if none of the allotment gardeners I interviewed felt a direct threat to their allotment garden, all of them felt that the situation might change with increasing pressure from other interests in the future. The protection of the allotment gardens and other disregarded urban green areas might be strengthened if their importance for biodiversity was recognized. For example, in the five most urban allotment gardens together we found eleven species of bumble bees (*Paper III*). This is a rather high number considering that only eight and four species of bumble bees were found in agricultural landscapes in Germany and the Netherlands respectively (Steffan-Dewenter et al., 2002; Kleijn & van Langevelde, 2006). Further, most other studies of bees in urban areas found a much lower number of bumble bee species, 4-6 species (Tommasi et al., 2004; McFrederick & LeBuhn, 2006; Matteson et al., 2008). This suggests that Stockholm is a rather bumble bee friendly city. In order to support a relatively high number of bumble bee species within the city also in the future, urban planners must become aware of the importance of areas with high diversity, such as allotment gardens, and also actively plan the larger urban landscape for the benefit of these species.

Conclusions

I found that urbanization decreases diversity of bumble bees, birds and trap-nesting insects. The local habitat quality and management of urban green areas affected the species composition of birds and abundance and species composition of bumble bees. Therefore both local habitat quality and the composition of the surrounding landscape are important for the studied organisms, the former mainly for abundance and the latter for species richness and to maintain a large species pool.

Management at both a local and a landscape scale is important. It is positive that Stockholm still harbours many bumble bee species, but without proper management and planning this will not continue to be the case. For example, the diversity of trap-nesting insects, which are predicted to respond to landscape changes at smaller scales than most bumble bees, was low in urban green areas.

To favour bumble bees, trap-nesting insects, and birds within cities it is important to improve the qualities of urban green areas as habitat for these species. Further, it is important to keep a variety of green areas within the city, and to enhance the connectivity among green areas within the city and with those in the hinterlands. Planners should recognize urban green areas that are normally overlooked in green plans of the city, such as allotment gardens. These areas have a large potential for biodiversity conservation within cities. Planners should also recognize the knowledge among managers of these green areas.

One of the most important achievements of the interdisciplinary work in this thesis was the contact with people that actually plan and manage urban green areas. It is crucial for biodiversity conservation and the future development of green areas in human-dominated landscapes to bridge the gap between ecologists and the people that directly, through management, influence these ecosystems.

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