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Bird communities in urban green space: Effects of habitat patch size, vegetation structure and urbanization gradient

Diploma thesis

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ABSTRACT

The urbanization affects the natural ecosystems as the human population grows all over the world. Urban ecosystems gradually expand and cover a considerable amount of the Earth´s surface. However, their influence on other ecosystems is considerably larger, however not very well understood. My research conducted in Prague, Czech republic has focused on the influence of vegetation and other habitat attributes, overall patch size and urbanization gradient on species richness of local bird communities. After corroborating the prominent role of the overall patch size and distance to the city margin in determining overall urban bird species richness as well as the richness of different species guilds, I focused on the influence of vegetation characteristics and other variables on the very local level. These are becoming increasingly interesting, since large scale management actions are not very feasible in cities. The proportion of area coverd by herb layer, tree species richness and presence of water bodies are the most important variables affecting the bird speciess richness. Correlations of these variables with other factors lead to alternative conclusions regarding the role of shrub cover, tree age structure and the potentially most valuable habitats to be conserved in the urban environment. Retaining as much natural habitat cover of native plant species with proper age class composition, avoiding unnecessary paving and retaining natural vegetation along water bodies seem to be the most feasible management measures to be taken in order to support richer bird communities in Prague. Many relatively sensitive bird species belonging to the insectivorous, specialist and ground-nesting guild could benefit from such activities. Retaining older tree age classes and the preservation of richer shrub cover are supposed to compensate for effects caused by the overall small size of central remnant forest patches and parks. However, further examination is needed to find out details about the legitimacy of this hypothesis in the highly dynamic and variable urban environment.

Key words: urban birds, species richness, guilds, vegetation structure, urbanization gradient, patch size, fragmentation

ABSTRAKT

Urbanizace ovlivňuje přírodní ekosystémy v důsledku celosvětového růstu lidské populace. Urbánní ekosystémy expandují a zabírají značnou plochu zemského povrchu. Jejich vliv na modifikaci přírodních procesů je podstatně větší, ale dosud ne úplně dostatečně studován a chápán. Ve své práci jsem se soustředil na výskum posouzení vlivu základních charakteristik prostředí a vegetace, velikosti zelených ploch a gradientu urbanizace na druhovoru bohatost ptáčích společenstev v hlavním městě České republiky v Praze. Potvrdil jsem klíčovou roli velikosti zelených ploch a jejich vzdálenosti od okraje města na celkovou druhovou bohatost ptačích společenstev. Tyto parametry měly zásadní vliv na druhovou bohatost různých guildů definovaných dle životních strategií a ekologie jednotlivých ptačích druhů. V dalším kroku jsem se soustředil na vliv charakteristik vegetace a dalších proměnných na složení ptačích společenstev na lokální úrovni. Tyto vlastnosti jsou důležité pro plánování konkrétních managementových zásahů, protože velkoplošné zásahy nejsou dobře proveditelné v městském prostředí. Podíl pokryvnosti bylinného patra, počet druhů stromů a přítomnost vodních těles jsou nejdůležitejšími proměnnými určujícími druhovou bohatost ptačího společenstva. Korelace těchto veličin s dalšími proměnnými prostředí vedou k alternativním vysvětlením týkajícím se role keřového patra, věkového složení stromového patra a potenciálně nejhodnotnějších habitatů v městském prostredí z hlediska druhové bohatosti ptačích společenstev. Zachování přírodní vegetace s přirozením druhovým složením a věkovou strukturou, vyhýbání se dláždění a zachování přirozené vegetace kolem břehů vodních těles se zdají být nejsnáze vykonatelnými opatřeními vedoucími k podpoře druhově bohatších ptačích společenstev v Praze. Mnohé poměrně citlivé druhy hmyzožravců, specialistů nebo na zemi hnízdící druhy jsou těmito aktivitami podporovány. Zachování starších věkových kategorií stromového patra a keřů v podrostu hypoteticky zmírňují negativní efekty způsobené malou velikostí zelených ploch v centrálních oblastech města. Je však potřebný další výzkum pro ověření těchto předpokladů.

Klíčová slova: městské ptáky, druhová bohatost, guildy, struktura vegetace, gradient urbanizace, velikost plochy, fragmentace

1. INTRODUCTION

The urban human population has increased rapidly during last decades around the world, from approximately 0,74 billion in 1950 to 3,16 billion in 2005 according to the statistics published by the United Nations (The 2007 Revision Population Database). This increase is accompanied by the spatial growth of densely built-up areas. The urbanization of natural habitats transforms the whole landscape and large areas of a new environment type arise recently. It is formed by both natural and human induced processes. The role of such urban ecosystems is becoming increasingly important at the global scale not only because of the growing area it covers. They provide a lot of direct and indirect benefits to the human society, since also urban ecosystems offer ecosystem services *(Constanza et al. (1997; Bolund and Hunhammar 1999).* Furthemore, the quality of the urban environment, where many people spend the majority of their time, has an indirect influence on the management. Specifically, 'healthy environment' could indirectly influence exploitation of different natural resources through shaping the education of city inhabitants *(Savard et al. 2000)*, as well as the opinions and attitudes of decision makers *(McKinney 2002).*

Nevertheless, the natural areas in urban ecosystems such as remnant forest patches or water bodies, should be preserved in natural condition and as diverse as possible, because diversity promotes sustainability in the long term *(Loreau 2000).* The preservation requires an adequate knowledge, so the urban planners and managers can retain or restore at least the most important features of high-quality habitats. To achieve the knowledge necessary for qualified management decisions, it is needful to focus on investigating different groups of organisms in order to gain insight into the whole studied ecosystem.

The birds belong to the most suitable organisms to be studied in the urban ecosystems for a variety of reasons. Considering the influence on the public, the scientific results regarding birds are relatively easily understandable amongst the people *(White et al. 2005).* Besides, birds can act as flagship species in the urban context *(Caro and O´Doherty 1999).* This fact is advantageous and it is needed to publish further information, because as *Peterson et al. (2009)* stated, it is highly desirable for the public to know also the actors providing the ecosystem services, not only the services themselves. According to these authors, the awareness of the exact roles of specific organisms may lead to their better protection.

From a more practical point of view, the birds are an excellent proxy for the evaluation of habitat quality in different environments. Their importance becomes even more pronounced in the urban environments, because a strong habitat loss and fragmentation effect emerges. The birds are able to respond to changes in the habitat quality relatively quickly because of their high mobility. Although the fragmentation of habitats tends to alter their population dynamics *(Andrén 1994)*, this influence is probably less important compared to other organisms with impaired mobility. On the other hand, if we focused on other good dispersers, such as some insect species, lichen or moss species, the detected responses may inform us just about much narrower environmental conditions than it is in the case of birds. The reasons for this are mainly the birds´ higher position in food chains, high spatial requirements, metabolic rates and energy consumption *(Nagy 1987)*. The birds therefore respond to habitat alteration in a more complex way and their populations are affected by relatively more factors than the smaller organisms. Moreover, birds are well detectable and we are able to estimate relatively easily not only the species composition, but also their abundances *(Savard et al. 2000, Marzluff 2005)*. Mammals are not such effective dispersers (except of bats) and their detection is much more complicated. In this sense, the birds seem to be an outstanding group for the research conducted in the urban environment, and provide a quick and effective hints applicable to the management of urban green space. Consequently, they can act as umbrella species *(Caro and O´Doherty 1999)* and are of great importance also for the management of other organisms.

2. URBANIZATION

The growth of urban population associated with the expansion of areas affected by human activities and covered by man-made constructions, is the phenomenon known as urbanization. This process is becoming increasingly intense as it is obvious from the information published by the United Nations (The 2007 Revision Population Database). Despite its great effects, the variety of consequences on natural processes remains poorly understood *(Chace and Walsh 2006)*. One of the crucial attributes of the urbanization process is that it generates a novel ecosystem type. The newly emergent type of environment really deserves the designation of an ecosystem as *Tansley (1935)* defined it *(Pickett and Grove 2009)*.

Although the urban ecosystems are mostly perceived as non-natural habitats by majority of people, this problem may pose a considerably difficult philosophical controversy. The main problem is whether human beings are or they are not considered to be an ecological equivalent of other organisms *(Collins et al.2000).* Apart from this issue, we are facing a fact of a human created environment being unfamiliar for many species, since it has been created quite recently. Urbanization started around 4000 B.C. in the Near East as a consequence of the neolithic revolution (which started about 8000 B.C.) *(Killen and Jonas 1998).* It is difficult to discuss about its general positive or negative nature. The urban environment undoubtedly offers many advantages from the human point of view in the economical and also cultural sense. These result from the mutual cooperation enabling the development and advances of the human society. On the other hand, the main problems of urbanization are connected with the restriction of natural habitats and their very rapid conversion and degradation. The rapid habitat alteration at the same time offers an opportunity to investigate the processes shaping the community assemblages of different groups of organisms, and their ability to respond and adapt to novel conditions. Hence, this ecological experiment *(Emlen 1974; McDonell and Picket 1990)* offers us the possibility to discover details about the functioning of human-disturbed ecosystems. As a result, a good starting point for sustainable management of urban ecosystems might arise and the management of other ecosystems can be inspired by the knowledge acquired by studying urban ecosystems *(Savard et al. 2000).*

The urbanization is the most prominent cause of the phenomenon denoted as the biotic homogenization *(McKinney 2006).* The crucial role of urbanization in this respect has been documented by numerous studies *(Devictor et al. 2007; Evans et al. 2009).* It specifically leads to the simplification of urban bird communities *(Clergeau et al. 2006),* i.e. to the decrease of bird species richness *(Hohtola 1978).* In addition, the local native species are predictably disappearing as the urbanization advances *(Donnelly 2002),* and are replaced by widespread and often non-native species *(McKinney and Lockwood 1999). Beissinger* and *Osborne (1982)* quantified in Oxford, Ohio, that the six most abundant urban bird species comprised 78% of the individuals and about 84% of the overall biomass. In contrast, in natural woods the six most abundant species comprised 48.5% of the individuals, and only 21% of the overall biomass. This example leads to a conclusion that a relatively few species thrive in markedly urbanized areas. Especially the population of exotic species are positively influenced by urbanization *(Crooks et al. 2004).* For example, the House Sparrow *(Passer domesticus),* European Starling *(Sturnus vulgaris),* and Rock Dove *(Columba livia),* which are all non-native to North America, largely dominated the urban ecosystem of Quėbec in Canada *(Clergeau et al. 1998).* They use the available resources effectively and in consequence, the overall bird biomass could be higher in urbanized areas in comparison to the natural sites (*Emlen 1974).*

The urban environment is undoubtedly extremely variable. The huge spatial variation in urbanization intensity from rural areas to city centres leads to the creation of urbanization gradients. Similarly to other environmental gradients, also the gradient of urbanization offers a good opportunity to study various ecological phenomena. Specifically, the urban gradient is suitable for studying, the role of humans and the impact of rapid habitat alteration to populations of organisms *(McDonnell and Pickett 1990)*.

The majority of researchers document a decrease in the species richness towards the more urbanized sites *(Beissinger and Osborne 1982; Clergeau et al. 1998; Marzluff 2005; Clergeau et al. 2006; Tratalos et al. 2007)*. One exception is the study of *Donnelly (2002)*, who reports an increasing number of bird species in middle and large sized forest patches at more urbanized areas. This result might be, however, an artefact of the study design as the author himself claims. However, the response of bird communities to the urbanization gradient is not fully monotonous. In congruence with the intermediate disturbance hypothesis *(Connell 1978)*, a higher species diversity at the transition zone between relatively natural and strongly developed urban habitat has been reported *(Blair 1996; Marzluff 2005; Aurora et al. 2009)*. The reason might be the formation of a certain "ecotone" between differently developed sites. *DeGraaf* and *Wentworth (1986)* speak about "middle habitat condition" between the two habitat types. Species occurring in natural habitats coexist on such ecotones with the species accepting the urban ecosystems or with species specifically adapted to them. Structures and resources originating from both natural and urban habitats bear the potential to support species belonging to either one of these ecosystems. On the other hand, *Turner et al. (2004)* expressed the uncertainty of whether the suburban diversity peaks are due to inherent factors or due to the proximity of natural areas.

Similarly to other studies, also *Tratalos et al. (2007)* revealed in Great Britain that the overall species richness peaks at sites with moderate housing density. However, the peak of non-urban indicator species emerged at very low housing densities. In this respect an important question arises, if it is sufficient to focus only on the overall species richness when estimating the value of a given site and of what conservational concern are the species occurring at the moderately developed sites. As *Blair (1996)* claims, many widespread species accumulate in this zone making its value minor than judged purely from the overall number of occurring species. Considering individual species or guilds is potentially a better option, when evaluating the importance and quality of habitats along the urbanization gradient.

Based on the positive relationship between specialist species extinction as well as their turnover rate (i.e. the rate of local extinction and recolonization events), and the level of urbanization, *Devictor et al. (2007)* pointed out, that the specialist species are at a higher extinction risk than the generalist species. Forest interior species may be considered as habitat specialists and accordingly, they were not present in the urban woods of Osaka Prefecture in Japan *(Natuhara and Imai 1999).* While the omnivorous guild and seed-eaters form a common part of the communities living in urbanized environments *(Beissinger and Osborne 1982; Clergeau et al. 1998),* the insectivores undoubtedly belong to the less abundant species. *DeGraaf and Wentworth (1986)* and others claim that urbanization causes the decline of insectivorous bird species in local bird communities. For example the densities of several insectivorous canopy feeders as well as the overall species richness of insectivores were lower in the urban environment than in the forest outside Oxford in Ohio *(Beissinger and Osborne 1982).* In San Antonio, Texas, the insectivorous birds were not present in the traditionally developed residential areas, built-up without regard to wildlife-friendly management decisions *(Aurora et al. 2009).* On the contrary, *Clergeau et al. (2006)* failed to find any difference in the number of feeding guild members between sectors with different levels of urbanization in European cities. Regarding the feeding substrate, these authors found the only difference in the bush-shrub habitat, with fewer associated species in the central parts of different cities. *Beissinger and Osborne (1982)* report that most of the ground feeders occur in the city of Oxford in Ohio. However, the most specialized species belonging to this group gradually disappeared from this area. *Clergeau et al. (2006)* considered also ground-nesting species and they revealed that such species were the least abundant in the central parts of European cities.

The loss of biodiversity and formation of unified communities of organisms caused by urbanization in cities are undesirable. On the other hand, it is probably very difficult to reverse this trend in the highly developed urban areas *(Evans et al. 2009).* One way to deal with this problem is to plan the future urban development in a way retaining more natural habitats. The situation in Great Britain illustrates the seriousness of the situation: the decline in bird species richness starts at much lower levels of household densities than it is currently planned to be built (*Tratalos et al. 2007).* As we can see, the effect of urbanization on bird communities is very strong. In some cases, the level of urbanization may even surpass the effect of patch size, as it was in the case of the neotropical migrants in Waterloo in Ontario, Canada *(Friesen et al. 1995).* However, the urbanization has a direct effect on the size of remnant patches through its fragmentation effect.

3. FRAGMENTATION OF HABITATS

As urbanization proceeds, a replacement of natural environment by a variety of artificial constructions and intensively managed habitats takes place and only remnants of original habitat remain undisturbed. However, these patches are more isolated and smaller than the original habitats. Therefore, the underlying mechanism of the fragmentation effects is attributable to the changes in remnant patch size and shape. Splitting of larger compact habitats to smaller patches leads to an increase in perimeter to area ratio. It is consequently accompanied by an increase in the area of edge habitats and intensification of edge effects. These effects are resulting from changes caused by adjacency of contrasting habitat types *(Sammalisto 1957 ex McCollin 1998). Murcia (1995)* classifies the edge effects as follows: 1. abiotic effects (consequences of the juxtaposition of distinct matrix); 2. direct biological effects (changes in abundance and distribution of species mediated by the physical conditions in edge habitats); 3. indirect biological effects (alteration of species interactions, e.g. predation, brood parasitism, etc.). *McCollin (1998)* considers edge effects mostly as changes in biotic interactions (competition, predation, brood parasitism), microclimate modification and structural changes in the vegetation cover. These effects are besides the physical changes attributable also to the level of isolation, which is defined by the degree of connectivity to other patches, their distance and the time since isolation *(Saunders et al. 1991).* Thus, the biogeographical changes associated with landscape fragmentation are accompanied with changes in the physical environment *(Saunders et al. 1991)* which both influences the whole ecosystems functioning.

The majority of organisms living in the original forests are negatively affected by fragmentation (*Murcia 1995).* This is true mainly for the species inhabiting forest interiors and requiring large amount of relatively undisturbed habitat. Loss of the most sensitive species from small forest patches is reported from a variety of urban environments (reviewed by *Fernández-Juricic and Jokimäki (2001); Lampila et al. (2005)).* The birds are highly mobile in comparison to other organisms and they are able to move relatively easily from patch to patch. The adverse effect of fragmentation thus might be linked to spatially scattered resources, rather than to their inability to migrate between patches *(Mörtberg and Wallentinus 2000).*

On the other hand, *Donnelly and Marzluff (2006)* revealed that forest aggregation at the landscape level is a less important determinant of the bird communities than the forest area and structure. Correspondingly, *Jokimäki (1999)* found in Oulu in Finland that isolation of patches, which is directly associated with the fragmentation, affects negatively only several species. In Valencia, Spain its effect appeared to be quite small as well *(Murgui 2007b)*. Also *Tilghman (1987)* found no effect of isolation on species richness in Springfield´s (Massachusetts) urban woodlands. In contrast, according to *Minor and Urban (2009)* even insignificant fragmentation events such as the construction of roads affect the bird communities residing in the separated patches. Despite the inconsistent conclusions about the role of habitat isolation, it is evident that the fragmentation plays an important role in shaping of bird community structure in the urban environment. At the same time, it is very difficult, if not impossible, to avoid habitat fragmentation in cities. Thus, the conservation management strategies have to concentrate on reduction of its negative effects. With respect to changes associated to fragmentation *(Saunders et al. 1991)*, the relatively easiest way, is to increase the connectivity between the isolated remnant habitat patches. The maintenance of greenways and trees along streets is relatively easy and effective course of action decreasing the impacts of habitat isolation *(Fernández-Juricic 2000; Fernández-Juricic 2001)*.

Studying the influences of habitat fragmentation, it is necessary to keep in mind, that the responses of birds to fragmentation are scale dependent *(Bolger et al. 1997)*. They might be linear on the local level, since local populations may diminish linearly with the retreat and fragmentation of their original environment. However, on the regional level, according to the metapopulation theory and the concept of the extinction threshold *(Hanski and Ovaskainen 2002)*, the response of the population complex might be non-linear. The individual populations might go extinct more rapidly, if the fragmentation reaches extreme levels and the habitat becomes too patchy and isolated. This knowledge leads us to the conclusion, that the retention of as large patches as possible and the enhancement of connectivity between remnants are the desirable and potentially executable measures to be taken in the urban environment.

4. HABITAT PATCH SIZE

The species-area relationship is a general tool used for predicting the number of species living in a distinct patch *(Tilghman 1987; Jokimäki 1999)*. In urban environment,the structure of 'forest' bird communities is largely determined by the woodland or park size *(Gavareski 1976; Natuhara and Imai 1999)*, because the probability of occurrence of many bird species in the remnant habitat patches is related to their area *(Mörtberg 2001; Donnelly and Marzluff 2004)*. Several theories try to explain the possible underlying causes of the species-area relationship. First of all, the larger the patch size is, the more species are likely to encounter a given patch and to settle there *(MacArthur and Wilson 1963)*. Thus the probability of patch occupancy for a given species rises with its area, which is known as the random placement hypothesis *(Arrhenius 1921)*. Another hypothesis regards the amount of available habitat types and resources. A larger patch potentially encompasses more heterogeneous habitat *(Williams 1943 ex Murgui 2007b)* and higher total amount of resources *(Wright 1983)*. This tends to be especially true in the urban environment, because it is highly dynamic and diversified per unit area, in comparison to the natural sites *(Evans et al. 2009)*. The third hypothesis considers the overall population size, which is likely to be larger in a bigger patch, ensuring higher population stability. Larger populations are thus more stable and less prone to (even stochastic) causes of extinction *(Hinsley 1995)*. Consequently, larger patches support relatively more stable populations of more species than small patches do.

The role of the habitat size is well illustrated on the example from Cambridge in Massachusetts, where nesting bird species richness diminished from 26 to 9 species over time, as habitat area declined due to urbanization *(Walcott 1974)*. The size of a patch, may also affect many other factors indirectly, e.g. through edge effects generating changes in biotic and abiotic factors (see chapter: Fragmentation). However, despite the area appears to be a significant factor determining the number of species living within a patch, other effects may override its influence under some circumstances. For example, *Friesen et al. (1995)* revealed a higher average diversity and abundance of Neotropical migrants in 4-ha woodlots than in 25-ha woodlots in the Region of Waterloo, Canada, resulting from different levels of surrounding urban development. It implies that the bird communities can be maintained or restored, when implementing the proper management practices or urban planning. Despite only the larger parks harbour the rarest species *(Murgui 2009)* and are more suitable to conserve biodiversity, the small parks can also aid the significant biological richness *(Husté et* *al. 2006).* Furthemore, they can favour dispersal *(Fernández-Juricic 2004)*, serve as stepping stones between larger patches *(Cornelis and Hermy 2004)* and definitely are of a certain appreciable conservation and aesthetical value *(Platt and Lill 2006).*

5. VEGETATION CHARACTERISTICS

5.1 Local vs. regional factors

The effects of vegetation physiognomy on bird communities tend to be influenced, besides the patch size and position on the gradient of urbanization, by an additional larger scale factor, i.e. the character of adjacent areas. It is reasonable to suppose, that the smaller the remaining patch is, the stronger would be the effect of its surroundings on the local bird community. This supposition is based on our knowledge regarding edge habitats, as documented e.g. in *Murcia (1995).*

The most important features of adjacent areas are the habitat types, their proportions, age and structure. The influence of surrounding habitats on bird communities living in urban green patches has been documented, however, the results of particular studies are controversial. *Jokimäki (1999)* pointed out the influence of broader-scale factors and the negative impact of built-up areas surrounding the forest patches. *Mörtberg (2001)* also reports a clear negative effect of buildings around coniferous forest patches on several bird species in Stockholm, Sweden, and *Tilghman (1987)* obtained similar results in urban woods in Springfield, Massachusetts. *Fernández-Juricic (2004)* suggests that the urban matrix surrounding the urban parks is usually of poor quality for woodland birds and can affect the bird populations by hindering the colonization process. *Minor and Urban (2009)* claim that the landscape level factors are of superior importance compared to the local vegetation features when predicting bird community composition. In contrast, the analysis of the breeding bird survey data from the United Kingdom does not indicate any noteworthy influence of regional factors on the urban avian assemblages *(Evans et al. 2009).* Similarly, *Husté et al. (2006)* stress the importance of local patch attributes, while no effect of the urbanization intensity around patches on the bird species richness has been revealed. A lack of any effect of the adjacent landscape type on the bird species richness has been reported already by *Clergeau et al. (2001).* Also *Donnelly and Marzluff (2006)* found in the neighborhoods of Seattle (Washington, USA) a stronger response of songbird populations to overall habitat quantity and local structure, than to habitat pattern expressed as the mean urban patch size and forest aggregation. Their finding is consistent with the statement, that the diversity of birds reflects features and amount of the vegetation rather than its spatial pattern at a larger scale *(Marzluff 2005)*. Therefore, it is still not very clear, whether the local (habitat quality) or regional (character of adjacent areas) factors are more important. Apart from this so far unsolved problem, focusing on the local features bears the potential to provide knowledge applicable for management or habitat restoration efforts at small scales. In contrast, the regional factors, such as patch configuration in the landscape, are difficult to manage.

Specifically, "local factors" include a number of small scale attributes of the environment, that influence the occurrence and abundances of birds. The most important factors are the number, density, complexity and volume of the vegetation layers, diversity of plant species, proportion of non-native plant species, surface covered by artificial objects, but also the presence of water bodies, the character of the terrain and its exposition etc. Many of these habitat features can be, and in fact are, influenced by management practices in urban green areas.

In contrast to local factors, broad-scale variables are disproportionately more difficult to manage in a developed city. Nevertheless, our knowledge about the spatial configuration of biotopes retaining or supporting the urban bird communities has the potential to be adopted in future urban planning.

5.2 Habitat management

Forests and other types of green patches in urban environment do generally not retain the qualities of the natural areas. Instead, the vegetation composition is determined by humans, is liable to variable fashion trends and availability of different plant species or by their ability to survive in the man-influenced habitats *(Whitney and Adams 1980)*. Moreover, the structure of the green patches is altered, because the layers are continuously managed and are not developing by means of natural succession. If the qualities of original habitats were preserved, some native species could persist without the necessity to develop new adaptations *(Fernández-Juricic and Jokimäki 2001)*. The "natural state" does not mean constant conditions. It rather means indigenous vegetation, natural structure and a different pace of changes as compared to the urban environment. The latter is considered to be highly dynamic *(Evans et al. 2009)*. The human caused changes tend to be much faster in contrast to the gradually developing conditions in the nature (exceptions being some catastrophes, i.e. natural disturbances). A good example of such changes is the rapid removal of dying trees from urban green patches, contrasting with the gradual decay of standing and later laying trees, or the mowing of the herb layer in urban parks, instead of its natural growth, development and consequent decay.

The magnitude of woodland species extinctions is dependent on the remaining vegetation cover attributes in urban areas *(Marzluff 2005)*. Therefore, there is an urgent need to develop management practices, mimicking natural processes and providing suitable space and long enough time periods for birds in order to develop the necessary adaptations. The response is likely to be phenotypic, i.e. behavioural, since birds are able to learn, for example to use new resources, relatively quickly *(Rutz 2008)*. The relatively easiest way to apply such a strategy is to retain as much indigenous vegetation cover as possible *(McKinney 2002)* and to manage it in a way ensuring the satisfaction of the birds´ minimal habitat requirements. The proper management activities can also ensure a reduction in the disturbance level *(Evans et al. 2009)*.

Nevertheless, almost all vegetation attributes in cities are under strong pressure exerted by land owners, urban planners and administrative units. Instead of leaving the plant cover to develop by the means of its own regulating forces and mechanisms, i.e. by the process of natural succession, urban planners prefer to determine the plant species composition, age structure, shape and amount of individual vegetation storeys. A certain need of meeting the aesthetical requirements of city dwellers exists. These demands are not always in concert with the natural condition of the vegetation. People tend to prefer regular curves, lines, shapes, distribution of plants, as well as lower densities of shrubs and trees because of enhanced visibility to greater distances. Unfortunately, the requirements advantageous for biodiversity are not the same as for the security of city inhabitants *(Sandström et al. 2006)* and a „neglected“ vegetation cover often conflicts with the aesthetical perception of the city inhabitants *(Fernández-Juricic and Jokimäki 2001)*. All the actions taken in order to maintain urban parks or forest remnants in the desired condition consequently change biotic and abiotic ecological factors. Management practices can strongly influence e.g. predation pressure *(Jokimäki and Huhta 2000)*, nesting parasitism *(Chace et al. 2003)*, competition *(Shochat et al. 2004)*, and through these also the nesting success *(Jokimäki et al. 2005)* and extinction rates *(Crooks et al. 2001)* of the urban bird populations. A chain of these changes probably causes a complex habitat and consequently bird community alteration.

Despite the unnatural conditions, the urban green space offers at least some contact with the nature for the city inhabitants. It is otherwise quite restricted in everyday life. Moreover, we cannot neglect the contribution of urban bird populations to the regional populations, especially in those species largely associated with urban environments *(Chamberlain et al. 2007)*. In addition, many of the urban bird species are of conservation concern *(Evans et al. 2009)*.

To be able to develop sustainable management strategies of urban green areas, we have to address questions, such as what vegetation features are the most important for bird diversity and what are the most suitable possibilities of their manipulation. The relatively well manageable attributes of green patches are the age and physical structure of the vegetation cover (incl. the diversity of plant species growing in different layers).

5.3 Age structure of vegetation cover

Based on the assumption, that the majority of urban green patches are managed actively by man, we can also assume that the plant community age composition is usually to some extent altered. It is definitely not easy to define the natural age composition. However, the selective removal of some age classes in urban areas implies a certain change in comparison to sites with the vegetation cover established by natural succession. The change potentially concerns the vegetation density, complexity, volume and through these factors the availability of feeding and nesting resources, as well as roosting and hiding places used by birds. It can be hypothesized, that food supply or nesting opportunities are improving with the increasing age of the vegetation, especially for forest specialist species. The hole nesting species such as the marsh tit *(Parus palustris)* and nuthatch *(Sitta europea)* showed association with older stands *(Mörtberg 2001)*, which implies the importance of older trees with more holes. Shrub nesting species preferred better developed and mature coniferous shrub layer in suburban neighborhoods in Massachusetts *(DeGraaf & Wentworth 1986)*, probably offering them higher-quality nesting substrate. Also in wooded streets, bird species diversity and partly also their abundances increase with the vegetation development *(Murgui 2007)*.

Donnelly and Marzluff (2006), who conducted their study in the Seattle metropolitan area, showed that young (less than 70 years old) tree stands, although dense, support different bird community than the older ones. The difference between these communities originate generally from diverse habitat requirements of individual bird species. Some species prefer older stands with mature trees *(Mörtberg and Wallentinus 2000)* and breeding bird species richness typically grows with the vegetation age *(Kocian et al. 2003)*. *Donnelly (2002)* hypothesizes, that the older patches potentially retain more sensitive bird species, which are also often listed as endangered species *(Mörtberg and Wallentinus 2000).*

In the urban space, longer time periods without human intervention occur only very seldom. The presumable consequence is a continuous disruption of ecological interactions among organisms and thus the absence of the most specialized species. These species often lack in urban woods, even though the vegetation volume is high and the layers are already well developed. *Willson (1974)* detected a certain threshold in the foliage volume and height diversity, above which no further increase in bird species diversity occurs. If any species appeared after this threshold, it may be due to the time needed for the establishment of more complex ecological interactions needful for these specialized species. If this is true, it indicates a certain ecological inferiority of urban woods in comparison to natural areas, because of frequent human intervention and consequent interruption of processes stabilizing the ecological relationships. *Natuhara & Imai (1999)* provide some support for this idea: the man-planted, at least 10 years old woods were of about the same quality as the older woods, with respect to bird diversity. However, these authors also report the absence of forest interior species and poorer establishment of the insectivorous guild in younger stands. The considerable influence of age is also documented in a study from Melbourne, Australia, which revealed a poorer establishment of the insectivorous and frugivorous guild in recently developed streetscapes as compared to older parks *(White et al. 2005).*

A principal methodological problem is how to measure the age of a given plant community. It is possible to perceive the age of green patches in the urban environment from two points of view: either as the age structure of the vegetation itself, or as the time period passed since the establishment of the whole patch. The difference might be not trivial, since in urban areas the management of the vegetation is pronounced probably more than anywhere else. Management practices would considerably change the age structure, compared to a patch established in natural conditions *(Natuhara & Imai 1999.* Thus the overall age of the green area (sometimes expressed as the time since the development started *(Donnelly and Marzluff 2006)*) might not be a satisfactory measure, and estimates based on DBH (diameter at breast height) might be preferable, as used e.g. by *Mörtberg (2001).* At the same time, estimation of actual age structure is also biologically more relevant assuming, that the birds perceive the age of the plant stands mostly by their volume.

In conclusion, the natural age class composition of plants ensures the diversity of vegetation features, and thus the variety of substrates used by birds. Moreover, the constrained management would facilitate the development of various ecological relationships.

On the other hand, *Donnelly (2002* and citations therein*)* do not advise to direct the management of all patches towards their climax stage, since some native species of birds may require younger stands. However, there is probably no reason to assume, that the urban environment lacks the disturbed and young patches of vegetation.

5.4 Vegetation structure and heterogeneity

Urban bird communities are substantially influenced by the proportion of vegetation cover, its structure and type *(White et al. 2005)*. However, the structure of plant communities inside the urban space is likely to differ from the natural communities. One of the reasons is the continuous alteration of the vegetation age structure. For example, the older stands tend to develop a higher level of canopy closure, which in turn affects all the underlying vegetation layers *(Willson 1974)*. Bird assemblages are consequently changing correspondingly to the vegetation structure determined by the successional stage of a given patch. The alteration caused by urbanization concerns also the physical structure of the vegetation cover directly, not just through its age composition.

The more complex vegetation cover aids the birds by providing more feeding and nesting substrates, as well as hiding places *(Marzluff and Ewing 2001; Fernández-Juricic 2000)*. Consequently a richer avifauna typically persists in such structurally diverse patches *(Tilghman 1987; Kocian et al. 2003; Evans et al. 2009)*. The increase in bird species richness is mainly attributable to forest passerines, because the more complex urban parks appear to be more suitable for them *(Fernández-Juricic 2004)*. *Sandström et al. (2006)* confirmed by study conducted in Örebro, Sweden, that the sites with the highest vegetation complexity constituted an environment suitable for the highest number of bird species and explained the lower avifaunal richness in residential and central areas mainly by the poorly developed vegetation structure.

Some studies operate with the term foliage height diversity to express the vegetation complexity. This parameter describes the vertical structural variability of the vegetation layers. Under certain circumstances, this factor alone suffices to explain the number of breeding bird species *(MacArthur 1964)*. *Gavareski (1976)* and *Lancaster and Rees (1979* in *Marzluff and Ewing 2001)* corroborated the correlation between foliage height diversity and the diversity of birds in the urban environment. Only *Jokimäki (1999)* obtained results inconsistent with these studies and found no effect of the foliage height diversity on bird species richness.

The vegetation complexity is closely related to the vegetation density, which is a significant factor in determining the habitat structure. It is a proxy for the overall amount of vegetation, with regard to its spatial configuration. No management is required to achieve the desired levels of dense vegetation in urban areas. The advantages of such a vegetation development without human intervention shows a study from Seattle, Washington, where several species requiring dense stands and sufficiently developed ground layer, occurred only in parks with unmanaged vegetation *(Gavareski 1976).*

The density of both the tree and the shrub layer enhances the breeding bird species richness *(Husté et al. 2006).* Higher tree density is one of the decisive factors ensuring the persistence of native forest bird species *(Donnelly 2002).* A study revealing that the parks in suburbs of Brisbane, Australia with sparser tree cover are not habitats of a sufficient quality for forest associated species *(Hudson et al. 1997* in *Chace and Walsh 2006)* supports this conclusion. Concerning the shrub layer, *Jokimäki (1999)* did not find any remarkable influence of the shrub density on the associated species. However, *Mörtberg (2001)* documented that e.g. the marsh tit *(Parus palustris)* showed some positive relationship to the dense shrub layer. In this respect, we should note that shrubs are typically denser than trees and should serve as a hiding place even for species usually not utilizing the shrub layer. From another point of view, it is not an unimportant fact when considering the colonization of isolated patches, that the dense vegetation cover within residential areas can act as a corridor for migrating birds *(Savard et al. 2000).* Taken together, it is desirable to maintain and support denser plant communities in the urban environment.

The visibility of nests of shrub-nesting birds determines to a great extent the risk of their predation and is negatively related to the amount of shrubs and the herb layer height *(Jokimäki et al. 2005).* Thus the density of the vegetation cover can increase the nesting success of urban birds. Similarly, *Marzluff and Ewing (2001)* concluded in their review that ensuring a sufficiently dense ground cover is important for breeding of many native birds.

Some authors consider the overall volume of the vegetation cover. It is an alternative measure to density, but the spatial distribution of the vegetation is neglected when measuring this factor. Generally, a higher foliage volume causes the addition of several bird species to the community *(Willson 1974)*, and the correlation between the woody plant volume and bird species diversity is strong also specifically in the urban context *(Mills et al. 1989; Aurora et al.2009).* However, *Willson (1974)* suggested a threshold of the amount of shrub and tree layer (about 50% together) above which the diversity decreases. However, this hypothesis has not been yet studied in the urban environment. It is disputable if this simple predictor would be a satisfactory indicator of species diversity in more complex urban environment.

According to *Willson´*s *(1974)* study from Illinois, after the ground layer develops well, one or two insectivorous species enrich the bird community. As the ground layer covered by lawns and weeds produces a big amount of seeds also seed eating guild could benefit from the development of this stratum *(Emlen 1974; Gavareski 1976).* However, the ground nesting species are typically not as abundant in central parts of cities as in the periurban areas *(Emlen 1974; Clergeau et al. 2006; Sandström et al. 2006).* Presumably the unsatisfactory condition of this layer, resulting from disturbances and management practices, causes this difference. Both higher tree and shrub cover are believed to enhance species diversity of bird communities *(Sandström et al. 2006; Fernández-Juricic 2004).* For example in North America, the development of the shrub layer may attract from one to four species and the tree layer development about twelve to fifteen species in comparison to sites with less developed layers *(Willson 1974).* This conclusion stresses the importance of vegetation maintenance in a more natural state. Unfortunately, the removal of shrubs is one of the most often used management practices in the urban environment *(Gavareski 1976).* Accordingly the species feeding or breeding on this layer occur in lower densities in central parts of the European cities *(Clergeau et al. 2006)*, or Singapore *(Lim and Sodhi 2004).*

5.5 Vegetation species diversity

Many forest bird species are more or less specialized to occupy deciduous or coniferous forests and this also determines their distribution. Therefore, the most important factor related to species composition of vegetation in urban areas is the proportion of deciduous and coniferous trees *(Jokimäki and Suhonen 1998).* The plant species diversity in either deciduous or coniferous forests seems to be not very important determinant of the habitat´s physical structure, except of it possible influence on the foliage density *(MacArthur and MacArthur 1961).* These authors refuse that the plant species diversity per se is a determinant of the bird species diversity in a deciduous forest. However, the more recent studies *(Jokimäki 1999; Husté et al. 2006; Fernández-Juricic 2004; Evans et al. 2009)*, except of study conducted by *Cornelis and Hermy (2004)*, suggest that species composition and diversity of vegetation could be a relevant factor influencing the response of bird communities. They showed a positive influence of tree and shrub (but not herb) species diversity on the number of bird species occupying the urban green patches (*Husté et al. 2006; Fernández-Juricic 2004), Evans et al. (2009)* who analyzed an extensive data set from the United Kingdom also confirmed this finding.

A negative effect of the tree species diversity on the bird species diversity is reported only from northern Finland, from Oulu *(Jokimäki 1999)*. However, it can be speculated that this could be attributable to the preferential planting of deciduous trees in this city (*Jokimäki 1996* in *Jokimäki 1999*) situated in boreal region dominated by coniferous forests. This variety of conclusions concerning the relationship between plant and bird species diversity shows that although the plant species richness may be an important factor, other features may be more significant.

5.6 Native vs. non-native vegetation cover

One of the most important factors determining the bird community composition, and one of the most easily manageable attributes at the same time is the presence of native or non-native plant species. The only effort, in order to maintain the original bird community, is to retain the indigenous flora and to avoid the planting of non-indigenous species. The successful plant colonizers, denoted as invasive species after entering the exponential phase of their expansion *(Pyšek 1995)*, exert often a great impact on the native flora and associated fauna *(Gurevitch and Padilla 2004)*. Bird species richness and abundance documented to decrease towards sites with exotic vegetation *(White et al. 2005; Donnelly 2002)*. The reason is possibly a lower density of herbivore invertebrates on these exotic plants. Also a study from the neighborhoods in San Antonio, Texas revealed a correlation of native bird species richness and diversity with the overall volume of indigenous plant species. Conversely, the non-native birds or non-territorial ones, increase their diversity and abundances with the volume of exotic vegetation *(Aurora et al. 2009)*. However, it is disputable, that the exotic species of plants and birds present in cities are of the same origin and therefore other factors are likely to be in the background of that correlation. We can hypothesize for example that non-native birds exert higher adaptability to novel conditions *(Duncan et al. 2003)*. For example, omnivores have an advantage when adapting to the urban environment *(Sandström et al. 2006)***.** Similarly some pre-adaptations may be responsible also for the prosperity of alien plant species, but no reason exists to assume the relation of exotic plant and bird species presence and invasion. The non-native birds may use resources becoming available, after the indigenous birds were not able to cope with the altered vegetation composition. For example, changes in food supply may be associated with such vegetation changes *(White et al. 2005)*.

Although ornamental shrubs seemed to replace to some extent the previously removed shrub layer *(Gavareski 1976), Tilghman (1987)* emphasizes that the native shrubs are likely to offer more niches and thus suitable environment for a higher number of bird species. Especially, many insectivorous bird species, that are generally quite heavily affected by vegetation alteration during the urbanization process would profit from native flora. Introduced tree species are usually not occupied by as many insect species as the native ones *(Southwood 1961)* and planted trees can not be a satisfactory habitat replacement for the insectivorous bird guild *(DeGraaf and Wentworth 1986)*. Although *Emlen (1974)* detected much more ground-gleaning insectivores in the neighborhoods in Tucson, Arizona, his results can be attributed to comparison with a desert habitat with a weakly developed ground layer. Apart from the actual causes of their influence, the alien plant species induce undesirable changes also within the bird community. In order to retain native bird species, it is necessary to maintain a high proportion of native to non-native plant species *(Marzluff and Ewing 2001)*.

6. AIMS AND HYPOTHESES

6.1 Aims

The primary aim of this study is to examine the role overall patch size, urbanization gradient on the overall bird species richness and species richness of different guilds and to separate their effects from the effects of other local variables. Specifically, from the influence of tree, shrub and ground layers, tree layer age structure and species richness as well as the presence of water body, position on the west to east and south to north continuum on and amount of built-up area.

Generally, the effect of green space size is considered to be clear in the urban context, because the results of many studies show consistently an increase in species richness and often also in abundances of birds (e.g. *Tilghman 1987; Fernández-Juricic and Jokimäki 2001; Mörtberg 2001)*. I have no reason to hypothesize otherwise, I expect to corroborate these results, although the recent approach is different. I examine the effect of overall patch size on the species richness and abundance on the very local level, i.e. inside a 100 m ring around each census point. I would like to find out some more details about the role of the smallest green patches (from ca. 0,1ha), which is still unclear, since so far mainly the medium sized and large parks or urban woods have been studied *(Gavareski 1976)*. There have been conducted several studies on wooded streets *(Murgui 2007; Fernández-Juricic E. 2000)*, which can provide further guidance. The effect of the urbanization gradient is controversial as discussed in the chapter: Urbanization. However, I assume an overall negative effect of this factor. Only some species are assumed to respond positively.

Some authors have come to conclusions suggesting local actions, that can be carried out to enhance diversity and abundances of birds in cities (e.g.: *Tilghman 1987; Fernández-Juricic and Jokimäki 2001; Donnelly 2002)*. However, I try to reveal the most important managable factors on the very local level, and generalize the neccessary measures, irrespective of the patch size and its position on the gradient of urbanization, which support the local avian species richness in Prague.

6.2 Hypotheses

1. The overall species richness is increasing with increasing proportion of the area covered by trees and shrubs providing more nesting and feeding opportunities.

2. Ground nesters probably need a developed shrub layer besides of ground layer, because the disturbance and predation pressure tends to be increased in the urban environment *(Jokimäki and Huhta 2000)*.

3. Shrub nesters and tree nesters need well developed shrub and tree layers respectively; tree nesters are also benefiting from a higher amount of available shrubs, since they provide aditional feeding substrate and hiding place.

4. Cavity-nesting species respond positively to the increasing age of tree layer, since older trees tend to provide more nesting holes. However, this relationship does not have to be particularly strong in areas, where artificial nesting holes are provided.

5. Insectivores are dependent on the insect species occurring in the urban environment, which in turn are dependent on the type and species composition of the vegetation cover. Thus, they are not necessarily influenced by the vegetation complexity, they rather response to the total volume of the vegetation.

6. Granivores prefer habitats with scarcer tree cover, richer ground cover and are benefiting also from lawns, because they can provide valuable food resources *(Emlen 1974; Gavareski 1976)*.

7. Omnivores are not as limited by specific food resources as granivores and insectivores. I hypothesize that the availability of their required nesting grounds may play a more important role, than the vegetation features determining a specific food resources availability.

8. Forest habitat specialists respond hypothetically to the proportion of tree cover and other factors are of inferior importance. Forest habitat generalist are not so tightly correlated with the tree cover as compared to specialists.

7. MATERIALS AND METHODS

7.1 Bird surveys and vegetation sampling

I conducted a point count of birds at 293 points in the city of Prague, from April until early June, in 2007 and 2008. All the birds seen and heard during the period of 5 minutes in a ring with the perimeter of 100 m were recorded *(Bibby et al. 2000)*. Each count point was visited three times, surveys have been conducted during morning hours (05:00 to 10:00). The count points were located in 114 green patches located across the whole city. They ranged in size from 942 m^2 to 3251449 m^2. The points were ordered from south to north and from west to east, to assign them arbitrary values of southernness or westernness.

The following vegetation attributes have been recorded at every point: % tree cover; % cover of tree classes defined by DBH (diameter at breast height), specifically < 10 cm, 11-30 cm, 31-50 cm and above 50 cm; % shrub cover and the three density classes (dense, middle, sparse); % herb cover and three density classes (dense, middle, sparse); % covered by buildings and pavement; presence of water body. Consequently, some other measures were calculated: ratio of coniferous to deciduous cover; the number of tree species (calculated as the number of species covering at least 5% of the surface in a 100 m circle around the counting point. If no such species was present, the tree species richness was set to 1). The ratio of patch perimeter to its size has been estimated.

The area of the urban parks and forest remnant patches was measured using the appropriate tool available at http://geoportal.cuzk.cz/wmsportal. The following structures were considered to be the patch borders: frequently used paved roads, railways, water bodies, such as ponds or the river Vltava (but not small streams inside the patches), blocks of buildings clearly demarcating the patch edge.

The city border was defined as the edge of continually built-up area of the city, where more than the 50% of the 1x1 km square area used for avifauna mapping in Prague *(Fuchs et al. 2002)* is covered by buildings *(Mourková unpubl. data)*. This is a biologically more relevant procedure, than the use of administrative city borders. The shortest distance of counting points to the nearest city edge was measured using maps (http://www.mapy.cz). The points located outside the city borders were assigned negative values in meters, and positive values to points within the built-up area of the city. This measure is considered to be more relevant than the distance to the city center, since the city of Prague is quite asymmetric in shape. Moreover, it can be considered as the proxy for migration barrier from outside the city to the given point.

Total number of the 42 species encountered at each census points during the three visits has been used for further analyses. 19 species of the 61 species recorded altogether have been omitted, because were either recorded at less than 4 census points or were not sufficiently surveyed. Specifically the building-nesting species such as Rock Dove *(Columba livia)* and Black Redstart *(Phoenicurus ochruros)*. The bird species were classified into groups according to their nesting and feeding requirements, migration status and specialization *(Hudec et al. 1983; Reif et al. 2007)*. (see Appendix 2). The species richness has been analysed, abundance of individual species was not considered. Abundances and species richness were highly correlated.

7.2 Statistical Analyses

The species richness at census points was the dependent variable and there was no need to transform it, to meet the assumption of normality. The explanatory variables were transformed to meet the assumption of normality of parametric tests. The percentages expressing the area covered by different type of vegetation layers or buildings, was transformed using arcsine transformation of the square root of a given quantity. The tree species richness was raised to the power of 2 and the overall area of a patch was log-transformed ($\log(x+1)$). The distance to the city margin was not transformed, because it included negative values, as it extended from locations outside the city to positive values assigned to locations within the city.

The basic statistics, as well as all the subsequent analyses, excluding the multivariate analysis were carried out using the R programming language (http://www.r-project.org/ , R version 2.8.1).

The generalized linear models were used to analyse the determinants of bird species richness, or the species richness of different guilds. The Poisson distribution of error terms and the log-link function was specified. The following variables were included in the maximum model: overall patch size, tree species richness, presence of water body, distance to the city margin, area covered by trees, shrubs, herbs and buildings). The stepwise regression procedure, using variable selection in both directions, has been performed. Based on AIC (Akaike information criterion) and the significance level of explanatory variables ($p < 0,05$), the minimum adequate model has been determined.

The analysis of individual species occurrence probability has been performed, using the generalized linear model. Specifically, the logistic regression on presence/absence data, with binomial error term distribution and logit-link fucntion has been carried out *(Sokal and Rohlf 1995).*

The multivariate analysis using CANOCO software was performed to determine the main trends in bird community composition *(Lepš and Šmilauer 2000).* The variable selection entering all the subsequent analyses, was based on the ecological relevance of the respective factors and on the principal component analysis (PCA) of explanatory variables. It revealed the most correlated explanatory variables. The following factors were selected: tree species richness, ratio of % cover of coniferous to deciduous trees, presence of water body, % area covered by trees in the four classes defined by their DBH (10cm, 30cm, 50cm, above 50cm), % area covered by shrubs, herbs and buildings. The initial DCA (detrended correspondence analysis; detrending by segments) was performed to determine the length of gradients. Based on its outcome, where the gradient lengths were well below 4, linear analyses proved to be performable *(Herben and Münzbergová 2003).* Species data were square root-transformed, centered and standardized prior to analyses. The patch size and the distance to the city margin have been used either as explanatory variables or as covariates, to reveal the importance of their influence. The patch area was also used as the grouping factor, in case permutation tests were performed, to account for possible autocorrelations between points laying in a single patch.

Two types of multivariate analyses were performed to analyze the species richness of different guilds: PCA (principal component analysis) with supplementary environmental variables and RDA (redundancy analysis). The indirect PCA ordered the dependent variables in the multidimensional space and the constructed axes are accounting for the highest variability in the dataset. The axes were additionally correlated with the supplementary environmental variables. RDA differs from the PCA method in being a direct gradient analysis. The ordination axes covering the highest variability in the dependent variables are directly correlated to the explanatory variables. Thus, the variation in the dependent variable comprised in a given ordination axis is directly attributable to the variation in the explanatory variable. The advantage of the comparison of these two methods is to reveal some hidden variability, which was not explained due to omitting some important explanatory variables from the analysis.

8. RESULTS

In total, I have recorded 60 bird species during the point counting in the city of Prague and 42 bird species have been considered for further analysis (see Appendix 1 for complete species list). The mean number of species occurring at one census point was 12.06 (SD = 2.76). The maximal number of recorded species 19 and the minimum was only 3 species.

Several explanatory variables were correlated with each other, as the preliminary principal component analysis (PCA) of these variables revealed (see Appendix 3). The explanatory variables for further analyses were selected with respect to these correlations. The tree cover, tree species richness and herb cover were correlated with one another; however, they were included in the analyses because their respective effects are of interest for my purposes. These variables are negatively correlated with the proportion of built-up area. The overall patch size is negatively correlated with the distance from the city margin meaning that patches tend to be smaller towards the city centre and larger towards its margin. The patch size is positively correlated with the length of the edge, since it is calculated as the ratio of patch size to its perimeter. Older trees with DBH up to 50 cm tend to grow in larger patches nearer the city margin. Younger trees are associated with richer shrub cover, whereas older stands are not. The proportion of the cover of a specific layer is usually correlated with the proportion of area covered by its subcategories regarding age or density structure.

The generalized regression models with specification of Poisson error distribution and a log-link function, selected based on their AIC (Akaike´s information criterion), revealed the significance of several factors influencing the overall species richness or the species richness within species guilds defined according to life-history traits and ecology (see Appendix 2). The best models explaining the bird species richness are summarized in the Table 1. The significant factors and their effects are represented schematically in the Table 2. The patch size has a highly significant positive influence on the overall species richness (z = 4.561; p = 5.08E-06), the species richness of both forest habitat specialist (z = 6.481; p = 9.12E-11) and forest habitat generalist bird species (z = 3.67; p = 2.42E-04), insectivores (z = 6.513; p = 7.38E-11), cavity nesters (z = 5.152; p = 2.57E-07), short distance migrants (z = 3.697; p = 0.000218) as well as non-migratory species (z = 2.647; p = 0.00811) at census points (Tab. 1 and 2). In other words, the overall number of species at census points as well as the species richness (Fig. 1) of the mentioned species guilds increased with increasing patch size of woods and parks (Fig. 2: insectivores).

Table 1. Summary of minimum adequate models explaining the bird species richness in individual groups, selected using AIC (Akaike information criterion) and significance levels of respective explanatory variables ($p < 0.05$).

Guild	factor	z-value	p-value
specialists	size	6.481	9.12E-11
	tree spp.richness	2.721	0.00652
generalists	size	3.67	2.42E-04
	distance to margin	-2.525	0.011557
cavity nesters	size	5.152	2.57E-07
	shrub cover	-2.53	0.01142
ground nesters	distance to margin	-4.009	6.10E-05
	buildings	-5.327	1.00E-07
shrub nestesrs	water	2.171	2.99E-02
tree nesters	-	-	-
long dist. migrants	herb cover	3.167	0.00154
non-migrants	size	2.647	0.00811
short dist. migrants	water	2.16	0.030768
granivores	herb cover	-3.48	5.02E-04
insectivores	water	2.766	0.005672
omnivores	distance to margin	2.281	2.25E-02
	herb cover	2.133	3.29E-02
	south-north	2.733	0.00628
	west-east	2.039	0.0415
	water	2.819	0.00482
overall spp. richness	area	4.561	5.08E-06
	margin	-1.97	4.88E-02
	water	2.314	0.0207

Table 2. Significant explanatory variables influencing the the overall species richness of birds and the richness of individual bird species guilds in Prague.

	overall spp. richness	insectivores	granivores	omnivores	long dist. migr.	short dist. migr.	non-migrants	cavity nest.	ground nest.	shrub nest.	tree nest.	specialists	generalists
area	■	■				■	■	■				■	■
distance to margin	■	■		■		■			■				■
tree spp. richness												■	
tree cover													
shrub cover								■					
herb cover			■	■	■								
buildings									■				
water	■	■		■		■				■			
S-N				■									
W-E				■									

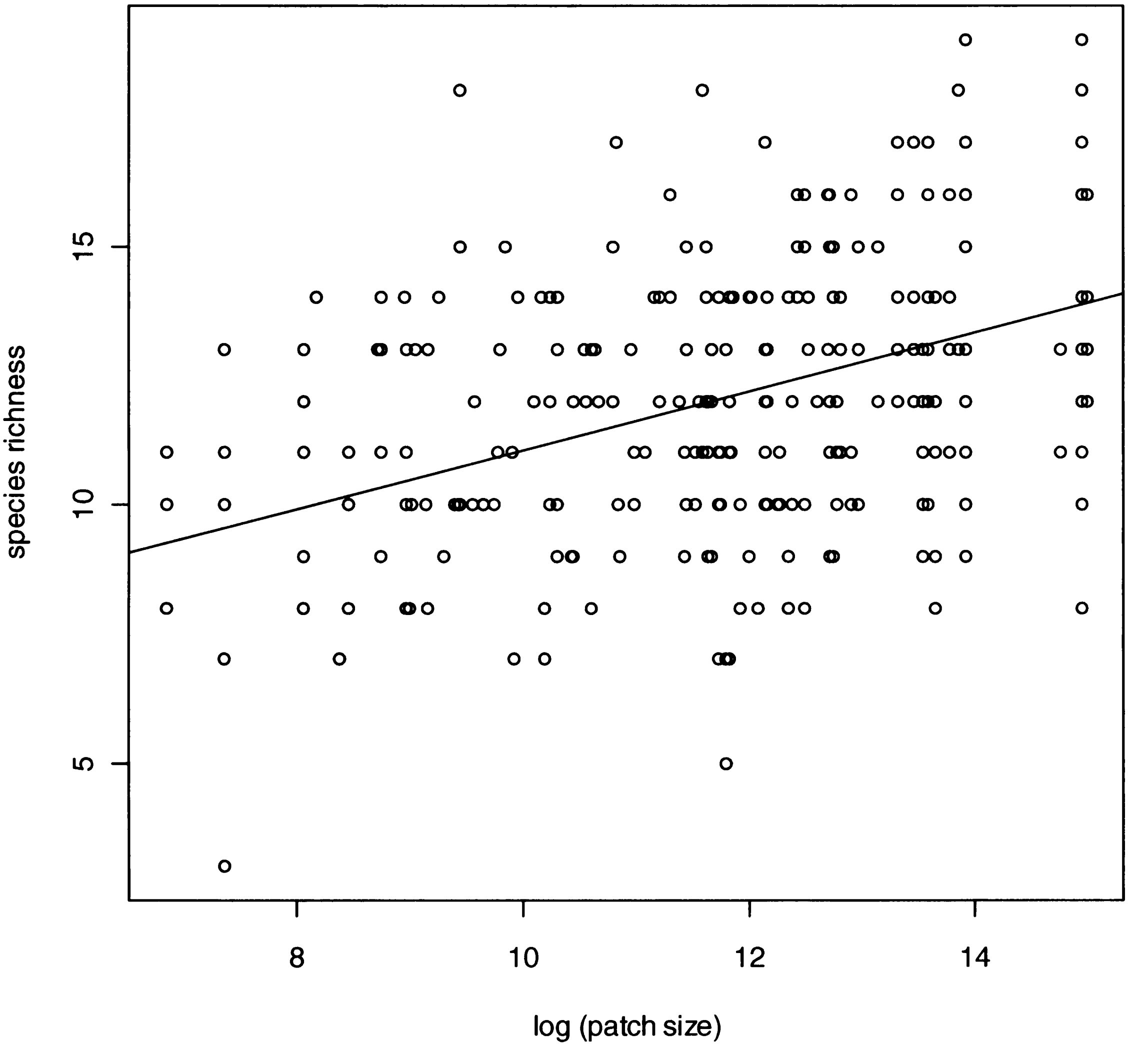

Figure 1. The species richness on individual census points grows with the overall size of the patch encompassing a given point (r = 0.41; p = < 0.001; d.f. = 291).

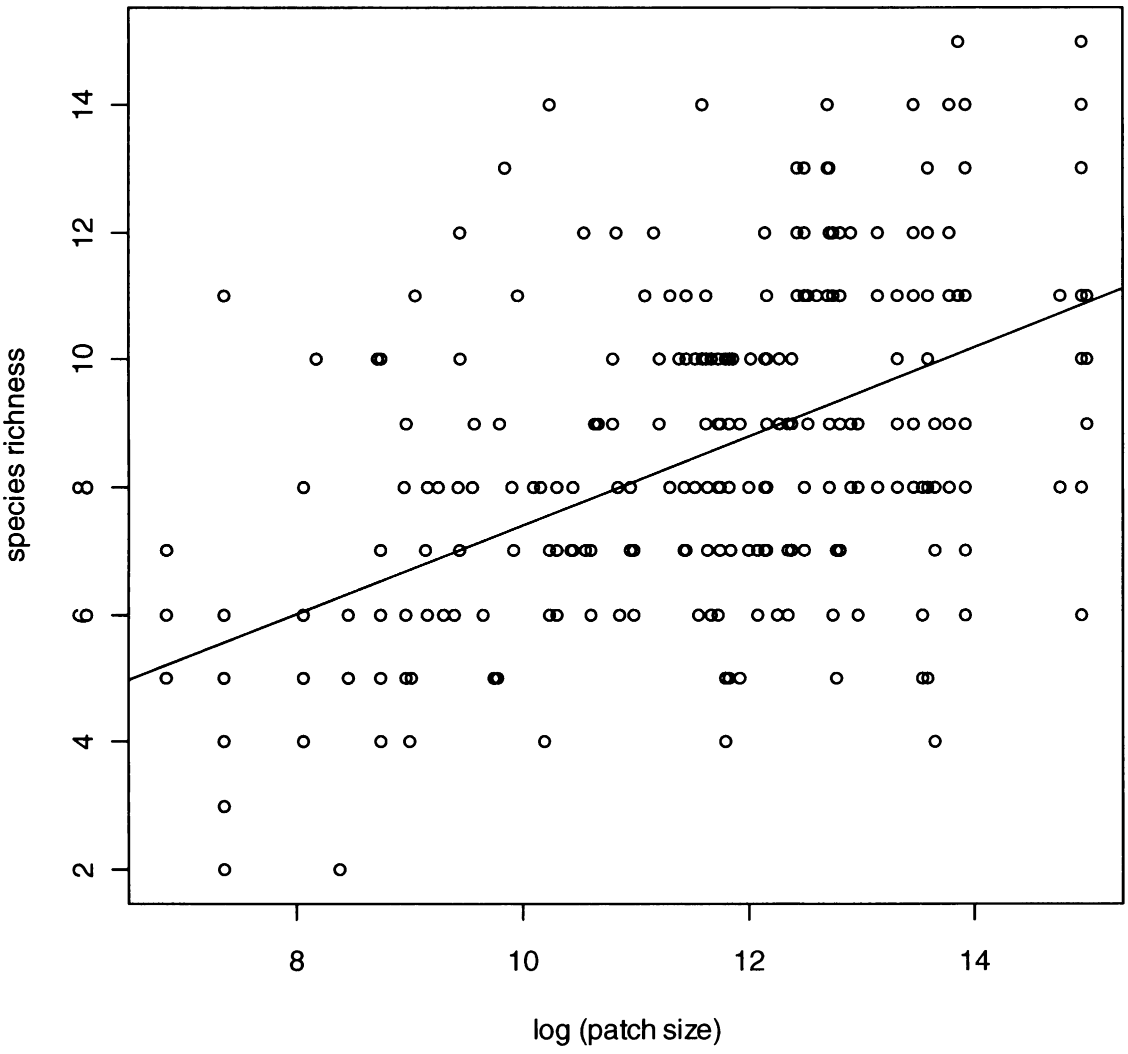

Figure 2. Species richness of the insectivorous species guild increases with overall patch size ($r = 0.52$; $p = < 0.001$; d.f. = 291).

The distance of a given point to the city margin roughly expresses the level of urbanization growing towards the city centre (urbanization gradient). Alternatively, it could be a proxy for a migration barrier, affecting the occupancy of patches with different position within the urbanized area. The overall species richness ($z = -1.97$; $p = 4.88E-02$), the species richness of generalists ($z = -2.525$; $p = 0.011557$), short distance migrants ($z = -2.259$; $p = 0.023894$), insectivores ($z = -3.563$; $p = 3.67E-04$) and ground-nesting birds ($z = -4.009$; $p = 6.10E-05$) decreases towards city centre, whereas the number of omnivorous species has been positively influenced by urbanization gradient ($z = 2.281$; $p = 2.25E-02$) (Tab. 1 and 2).

The overall bird species richness of census points was significantly influenced by the presence of water bodies – river, ponds (z = 2.314; p = 0.0207). Specifically, the number of shrub-nesting (z = 2.171; p = 2.99E-02), insectivorous species (z = 2.766; p = 0.005672), omnivorous (z = 2.819; p = 0.00482) and species migrating to short distances (z = 2.16; p= 0.030768) increased significantly, when a water body occurred within the area of a census point (Tab. 1 and 2).

The amount of herb cover had no effect on the overall species richness. However, it influenced positively the number of long distance migratory species (z = 3.167; p = 0.00154) and granivores (z = -3.48; p =5.02E-04). On the other hand, the number of omnivorous species decreased with increasing herb cover (z = 2.133; p = 3.29E-02). Birds nesting on the ground were less common at sites with a higher amount of buildings or paved surface (z = -5.327; p = 1.00E-07). The number of specialist bird species has been positively influenced by the tree species richness at census points (z = 2.721; p = 0.00652). The position of census points on the south to north and west to east gradient within Prague significantly influenced only the number of omnivores. Their species richness increased from W to E (z = 2.733; p = 0.00628) and from S to N (z = 2.039; p = 0.0415).

The multivariate analysis of the entire community reduced the variability in my dataset to several axes, which were constructed with respect to the variability directly explicable by the explanatory variables. The redundancy analysis (RDA) thus explained 10.7% of the variability. After the effects of patch size and the distance to the city margin were accounted for using them as covariates, only 5.3% of the entire variability was described by the ordination axes (Fig. 3). The conditional effects of herb cover (F = 5.56; p = 0.004), presence of water body (F = 2.46; p = 0.01) and tree species richness (F = 2.16; p = 0.02) remained significant after the covariates were considered (Tab. 3).

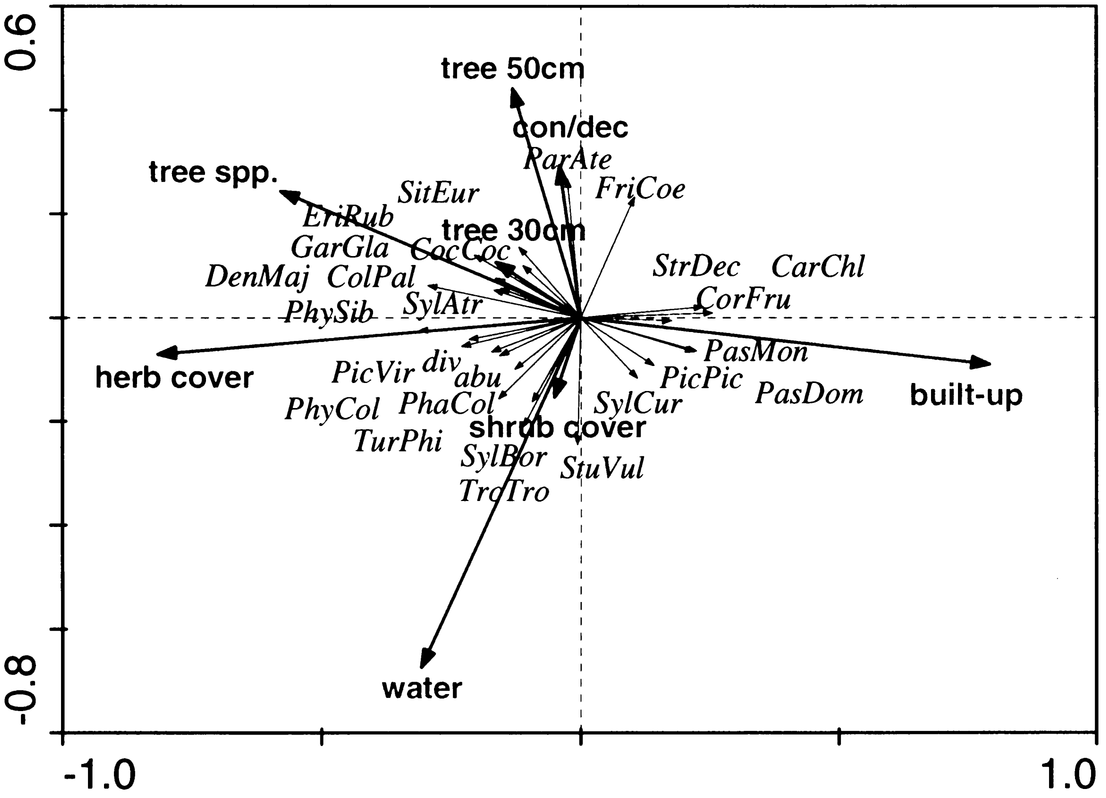

Figure 3. RDA ordination diagram of the whole bird community (sum of all canonical eigenvalues = 0.053; covariates: size, distance to the margin; forward selection; Monte Carlo permutation test – 499 permutations, blocks defined by covariable: size)

Table 3. Forward selection output: RDA of the whole community species richness - covariables: size, distance to margin (conditional effects; Monte carlo permutation test – 499 permutations)

Variable	Var.N	LambdaA	P	F
herb cover	24	0.02	0.004	5.56
water	29	0.01	0.01	2.46
tree spp. richness	17	0	0.02	2.16
tree 30 cm DBH	13	0.01	0.236	1.46
tree 50 cm DBH	14	0	0.744	1.1
coniferous/deciduous	16	0	0.202	1.25
shrub cover	18	0.01	0.494	1.38
built-up area	28	0	0.084	1.12

Table 4. Forward selection output: RDA of the whole community species richness (conditional effects; Monte carlo permutation test – 499 permutations, blocks defined by covariable: size)

Variable	**Var.N**	**LambdaA**	**P**	**F**
size	7	0.03	0.002	10.19
herb cover	24	0.03	0.002	7.79
distance to margin	6	0.01	0.002	4.15
water	29	0.01	0.002	2.46
tree spp. richness	17	0.01	0.002	2.16
tree 30 cm DBH	13	0	0.058	1.46
tree 50 cm DBH	14	0.01	0.312	1.1
coniferous/deciduous	16	0	0.226	1.25
shrub cover	18	0	0.086	1.38
built-up area	28	0.01	0.244	1.12

The ordination diagram divides the bird community with respect to the urbanization gradient along the first axis. The total proportion of herb cover and proportion of built-up area are negatively correlated, but they are both correlated with the first ordination axis. The overall bird species richness (spp) tends to correlated positively with the first axis and is quite closely correlated with the overall abundance (abu). The second axis differentiates the community to species requiring older stands and species which require more open habitats or shrubs and are somehow benefiting from the presence of water body. The european starling *(Sturnus vulgaris)* is atypically negatively correlated with older trees (tree 50 cm), however it may respond to the presence of water resource, or other unidentified variable.

The canonical axes constructed by RDA of species groups (Fig. 4) explained 16.8% of the entire variability, but only 6.7% after the patch size and distance to the city margin were designated covariates. The presence of water body alone remained significant ($F = 4.79$; $p = 0.006$) (Table 5. and 6.). The different guilds are overlapping in species composition. The extent of this overlap determines which guilds are responding to similar factors. The first axis of the ordination diagram divides the species richness of individual guilds depending on their positive or negative response to the urbanization gradient. From all guilds only one responds obviously positively to artificial constructions, i.e. to built-up area. Granivores are gaining species as the proportion of built-up area at census points increases. Conversely, the long distance migrants are forming a group with the most marked negative response to the urbanization pressure. Similarly, short distance migrants along with specialists, generalists and ground nesters respond positively to the proportion of herb cover and negatively to the artificial constructions. Omnivorous species are responding positively besides the herb cover also to the presence of water body. This variable is important also for shrub nesters along with the proportion of shrub cover. Cavity nesters, non-migrants and insectivores are positively correlating with species rich tree stands of older age. Tree nesters are responding similarly, but more strongly to the tree layer age.

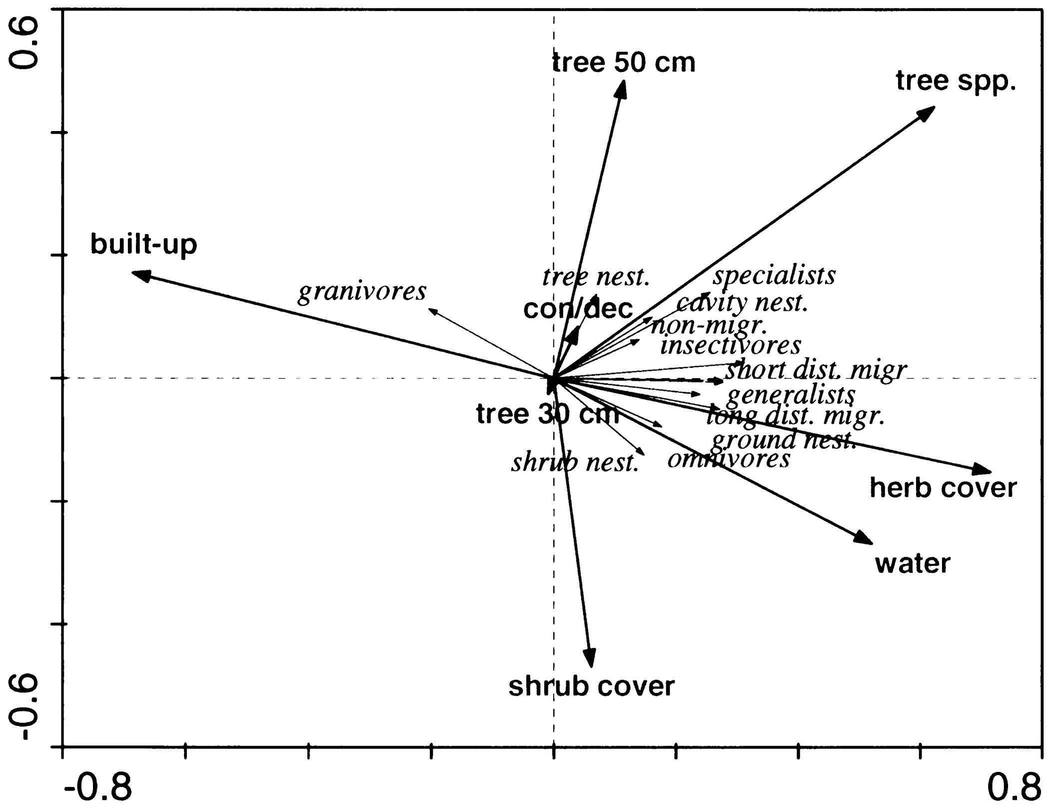

Figure 4. RDA ordination diagram of bird guilds (sum of all canonical eigenvalues = 0.067; covariates: size, distance to the margin; forward selection; Monte Carlo permutation test – 499 permutations, blocks defined by covariable: size)

Table 5. Forward selection output: RDA of bird guild species richness - covariables: size, distance to margin (conditional effects; Monte carlo permutation test – 499 permutations)

Conditional Effects				
Variable	**Var.N**	**LambdaA**	**P**	**F**
herb cover	24	0.03	0.294	10.35
water	29	0.02	0.006	4.79
tree spp. richness	17	0.01	0.068	3.59
shrub cover	18	0	0.686	1.09
tree 50 cm DBH	14	0	0.692	0.93
tree 30 cm DBH	13	0	0.716	0.58
built-up area	28	0.01	0.688	0.76
coniferous/deciduous	16	0	0.508	0.43

Table 6. Forward selection output: RDA of bird guild species richness (conditional effects; Monte carlo permutation test – 499 permutations, blocks defined by covariable: size)

Conditional Effects				
Variable	**Var.N**	**LambdaA**	**P**	**F**
herb cover	24	0.07	0.002	23.06
patch size	7	0.04	0.002	11.37
dist. to margin	6	0.02	0.002	7.78
water	29	0.02	0.002	4.79
tree spp. richness	17	0.01	0.008	3.59
shrub cover	18	0	0.358	1.09
tree 50 cm DBH	14	0	0.422	0.93
tree 30 cm DBH	13	0	0.77	0.58
built-up area	28	0.01	0.564	0.76
coniferous/deciduous	16	0	0.864	0.43

Multivariate analyses using the RDA method and PCA method with supplementary variables were conducted for different species guilds. The drop in explanatory power of ordination axes in RDA in comparison to PCA with supplementary environmental variables illustrates that other factors, not included in our analysis can influence the species richness at census points (Tab. 7). It is possible to speculate, that the character of adjacent areas might be the most important explanatory variable not considered in recent analyses.

Table 7. Comparison of the variability explained by 4 axes using the PCA with supplementary environmental variables (axes constructed to explain the maximum variability in the dependent variable, without respect to explanatory variables) and RDA (axes constructed to explain the maximum variability in the dependent variable attributable to explanatory variables). The overall explained variability attributable to the explanatory variables (Sum of all canonical eigenvalues) is approximately equal in both cases.

		Axes: eigenvalues				Sum of all canonical eigenvalues
Method	Guild	1	2	3	4	
PCA+supplementary env.var.	diet	0.326	0.313	0.184	0.046	0.067
RDA	diet	0.051	0.008	0.007	0.001	0.066
PCA+supplementary env.var.	migration distance	0.398	0.271	0.14	0.074	0.063
RDA	migration distance	0.05	0.008	0.003	0.001	0.063
PCA+supplementary env.var.	nesting substrate	0.283	0.225	0.179	0.122	0.056
RDA	nesting substrate	0.035	0.01	0.006	0.002	0.056
PCA+supplementary env.var.	specialists/generalists	0.514	0.269	0.082	0.03	0.092
RDA	specialists/generalists	0.079	0.012	0.001	0	0.091

The logistic regression determined the probability of occurence of individual species depending on specific significant variables. Four species have been selected belonging to different guilds (Table 8, Appendix 4). The jackdaw *(Corvus monedula)* is occurring with higher probability closer to the city centre. The chaffinch *(Fringilla coelebs)* is not present only in the smallest patches and responds negatively to a higher shrub undergrowth cover. The willow warbler *(Phylloscopus trochilus)* prefers areas with a higher tree species diversity and the winter wren *(Troglodytes troglodytes)* responds positively to a variety of factors including patch size, proportion of tree cover with 50 cm DBH, the presence of water bodies and the distance to the city margin, which is affecting this species negatively.

Table 8. Logistic regression models predicting the probability of occurrence of four selected bird species.

Species	Probability of occurence
jackdaw *(Corvus monedula)*	0.01978152 + 1.000817 x (distance to margin (m))
chaffinch *(Fringilla coelebs)*	5.30853 + 1.000002(size (m^2)) + 0.08803726 (% shrub cover)
willow warbler *(Phylloscopus trochilus)*	0.05234001 + 1.536307 (no. of tree species)
winter wren *(Troglodytes troglodytes)*	0.06222561 + 1.000001 (size (m2)) + 0.9995242 (distance to margin (m)) + + 9.681433 (% tree 50 cm DBH) + 6.22993 (presence of water body)

9. DISCUSSION

The worldwide process of urbanization largely affects also the region of Prague, the capital of Czech Republic *(Ouředníček 2007)*. Although the urbanization leads to a tighter human cooperation, which is an advantage with respect to the society, it often has adverse effects on the surrounding ecosystems. For example, the urban bird communities are very well studied *(Fuchs et al. 2002)* by virtue of researchers´ concentration and cooperation in cities, but at the same time, the urban bird communities are negatively affected by strong urbanization *(Beissinger and Osborne 1982; Clergeau et al. 1998; Marzluff 2005; Clergeau et al. 2006; Tratalos et al. 2007; Devictor et al. 2007)*.

In conformity with the majority of previous studies *(Gavareski 1976; Tilghman 1987; Jokimäki 1999; Natuhara and Imai 1999; Mörtberg 2001; Donnelly and Marzluff 2004; Evans et al. 2009)*, my result suggest a dominant role of the patch area on bird species richness and community structure. I found that bird community is largely determined by the size of a wooded patch containing a given census point. It positively influences the overall species richness and the species richness of 6 (out of 12) species groups defined according to their specialization, migratory status, feeding and nesting requirements. The above mentioned studies considered the species richness of the patches as a whole and therefore confirmed the species-area relationship. However, I have studied the influence of patch area on species richness of a certain proportion of the patches, more specifically, on a census point with a perimeter of 100 m. This result shows that with increasing patch size more species tend to be present at every single count point. *Fernández-Juricic (2004)* obtained a corresponding result in Madrid in Spain, where species richness per unit area increased with the increasing patch size. These findings correspond to the hypothesis that more species are likely to occupy larger patches *(Arrhenius 1921; MacArthur and Wilson 1963).* This hypothesis might be particularly true in the urban environment, where the green patches constitute islands of suitable habitats separated by unsuitable environments *(Fernández-Juricic and Jokimäki 2001).* However, this hypothesis does not fully apply after the patch size decreases extremely, because other effects such as isolation become more pronounced and the species decline is not caused purely by habitat loss *(Andrén 1994).* Nevertheless, these hypotheses as well as hypotheses assuming more heterogeneous habitats *(Williams 1943 ex Murgui 2007b)* and more stable populations in larger patches *(Hinsley 1995)* has been suggested also for species other than birds.

My findings thus provide some support to hypothesis explaining the higher bird species richness in larger patches by higher total amount of resources *(Wright 1983).* I have identified that species richness of insectivorous species was significantly affected by wood patch size in Prague. I suggest that these birds might be typically affected by lower food resources, i.e. by lower diversity and abundance of insects in small patches. My data also do not support the hypothesis that the effect of the hypothesized lower diversity of insects can be compensated by their higher abundances in edge habitats *(Murcia 1995).* On the other hand, considering individual insectivorous bird species, their avoidance of small patches might be of behavioural origin or alternatively due to edge effects or other habitat quality correlates *(Murcia 1995; McCollin 1998)*, rather than due to insufficient resource availability. Some common species, such as *Parus major, P. caeruleus*, detected at 98.3% and 95.2% of points respectively, are primarily insectivores but thrive even in the smallest patches. Conversely, the winter wren *(Troglodytes troglodytes)* was occurring with a markedly higher probability in larger patches than in smaller ones. Further examination is therefore needed to evaluate the dynamics of insect and insectivorous bird communities and their relationships in urban habitat patches of various sizes.

Furthermore, it is important to note that in Prague the average age of tree stands correlates positively with patch size. The effect of patch area on bird species diversity might be thus to some extent confounded with the vegetation age since some species are associated with older stands *(Mörtberg and Wallentinus 2000)* and the overall species richness is positively related to the vegetation age *(Kocian et al. 2003)*. Disentangling the respective role and importance of these two factors is an interesting issue. If the influence of old trees is strong enough, the proper and targeted management retaining older age classes may improve the attractiveness of small patches for some bird species. The negative effect of their overall small size might be thus to some extent compensated. Some species require older vegetation for nesting *(DeGraaf & Wentworth 1986)* and particularly cavity-nesting birds might respond to older vegetation composition *(Mörtberg 2001)*. In this study the cavity-nesting birds show some association with older trees afte the effect of patch size has been accounted for, although the relationship appeares not to be very tight. However, it is tighter considering tree nesters, which indicates, that older and larger trees are their prefered nesting substrate.

Sedentary bird species, as well as birds migrating to shorter distances are preferably occupying larger patches in Prague. In Stockholm, Sweden the same effect has been detected and *Mörtberg (2001)* suggests several explanations based on population stability, resource availability and colonization probability. I suggest that these effects might influence also the community of sedentary birds in Prague. Smaller and isolated patches might not sustain stable populations, which are weakly supported by immigration of individuals from more suitable sites *(Gustafson and Gardner 1996)*. They also could be of lower habitat quality and do not offer enough resources during the whole year *(Murgui 2007b)*. Taking into account differences in migratory status and patch occupancy depending on its size, I also hypothesize that non-migrants and short distance migrants have an advantage when colonizing urban patches of higher quality. The long distance migrants arrive later to their breeding grounds. They are hypothetically forced to occupy also smaller patches of habitats due to stronger interspecific competition in larger patches. Alternatively, they might have better ability to cross migratory barriers such as urban areas and therefore to occupy also smaller and isolated patches in city centre.

Both forest-dependent species groups classified according to their niche breadth as habitat specialists or generalists *(Reif et al. 2007)* were positively responding to the overall patch size. Since the generalist species were negatively affected also by the distance to the margin of Prague, it can be assumed that they are avoiding the highly urbanized areas, encompassing mainly small patches. In comparision to generalists the specialist species are more prone to extinction *(Devictor et al. 2007)*, but may take an advantage of large patch size, maintain more stable populations and thus persist there *(Hinsley 1995)*. The difference between forest habitat specialists and generalists deducible from the ordination diagram is that specialist species are correlated tighter with older stands with higher tree species richness, whereas generalist species do not show such an apparent association with any other variable except of the negative correlation with urbanization pressure and positive correlation with the proportion of herb cover.

The overall species richness of birds in urban woods and parks has been also negatively affected by urbanization, i.e. it decreases towards the city centre, which is in accordance to other studies *(Hohtola 1978; Beissinger and Osborne 1982; Clergeau et al. 1998; McKinney and Lockwood 1999; Donnelly 2002; Marzluff 2005; Clergeau et al. 2006; Tratalos et al. 2007).* More specifically, the insectivores, short distance migrants, ground-nesting species and generalists seem to be the most sensitive species groups with respect to the urbanization gradient. *DeGraaf and Wentworth (1986)* also report a decline in the species richness of insectivores, but do not suggest any possible explanation. *Denys and Schmidt (1998)* suggest that the decrease in food supply of insects towards more urbanized sites is mainly due to isolation of patches. However, management practices also certainly affect the insect community in cities, because a considerable number of insect species is associated with dead wood which is actively removed from urban remnant patches *(Ehnström 2001; Tyrväinen et al. 2003).* Moreover, intensive management and disturbations, including air pollution, could be responsible for the decrease of insect abundance in more urbanized sites. Apart from the fact that many short distance migrants are insectivores, the lower species richness of this group towards city centre could be also attributable to their unwillingness to cross unsuitable urban environments. The effects of the strongly urbanized matrix surrounding potentially suitable habitat patches even outweighed the effect of overall patch size, although this has been shown for long distance migrants in Waterloo, Canada *(Friesen et al. 1995).*

Consistently with other studies *(Emlen 1974; Clergeau et al. 2006; Sandström et al. 2006)* I found that the species richness of ground-nesting birds declines towards the central parts of Prague and also the higher proportion of built-up area has an adverse influence on their diversity. The intensive management practices (mowing, pavement etc.) resulting in destruction of suitable nesting substrates and a pronounced disturbance in central parts associated with higher predation risk (including dogs and cats) might enhance the deterioration of ground-nesting guild in cities *(Jokimäki and Huhta 2000).*

On the other hand, the omnivorous species guild seem to benefit from the proximity to the city centre. My finding supports the hypothesis that omnivory is advantageous for species facing urbanization and adapting to the urban environment *(Sandström et al. 2006).* These species are able to utilize a variety of food resources, thus are not constrained by the possible lack of a specific food type. They benefit from supplementary food resources such as ornamental fruiting trees planted in cities *(Beissinger and Osborne 1982)* or human-produced refuse *(Luniak 2004)*. Large proportion of this species group consists of corvids, which are suggested to be positively associated with the urban environment *(Jokimäki et al. 1996; Tratalos et al. 2007)*. They are able to adapt to close proximity of humans and benefit from variety of food supplies, lower densities of their predators and good nesting opportuinities (e.g. *Jokimäki 1999)*. They are also very adaptive by means of behavioural habituation to close proximity of humans. My logistic model for Jackdaw *(Corvus monedula)* supports these findings, since the proximity to the city centre was the best predictor of its occurrence probability. The increase in magpie *(Pica pica)* and jay *(Garrulus glandarius)* abundances during the last few decades in Prague also illustrate this phenomenon *(Fuchs et al. 2002)*. As omnivores benefit from the presence of water resources it can be hypothesized that due to their relatively larger body size they need sufficient and persistent water resources. Another curiosity regarding the omnivores in Prague is due to the fact, that no other species guild, except of this one, has responded to the position on the west to east and south to north gradient. I assume that this effect is due to the fact that other species of this guild are widespread throughout the city, but rook *(Corvus frugilegus)* was detected only in the north-eastern part of Prague. The significance of the W-E and S-N variable might be indicating the addition of this single species.

My results also show, that the specialists react positively to a higher number of tree species present at a sample point. Although, some generalist species might benefit from higher tree species richness. For example, more tree species present at a census point increase the probability of occurrence of the Willow Warbler *(Phylloscopus trochilus)* considerably. Different tree species provide a higher diversity of resources such as seeds, fruits, or are potentially associated with different insect communities. The dissimilar structure of various tree species might be also important. Especially coniferous and deciduous trees have a considerably different structure and character. Since some species require coniferous trees (e.g. *Certhia familiaris, Parus ater, P. cristatus*) the mixture of coniferous and deciduous trees might support more diverse bird communities. I also suggest that higher tree species richness increases the probability of individual requirement fulfilment of more species. The effective niche partitioning therefore enables coexistence of more species and support more diverse bird communities. However, exotic tree species presumably do not exert such a positive effect *(Aurora et al. 2009)*. The overall species richness of various foraging guilds of birds is negatively influenced (except some omnivores, *Beissinger and Osborne 1982*) by the presence of non-native trees *(White et al. 2005; Donnelly 2002)*. The proximate reason for the bird community impoverishment is attributable to the low number of insect species associated with exotic trees *(Southwood 1961)*.

Surprisingly, the proportion of the area within a 100 m ring covered by trees did not influence species richness of any guild. Presumably the age composition of trees may have a stronger influence on the tree-nesting guild species richness, since no other significant factors determining this group´s richness have been revealed. The proportions of area at each census point covered by individual age classes might be a better predictor. The multivariate analysis revealed an increasing trend in tree nesters species richness towards areas with higher proportion of older tree classes. Similarly, I have found no environmental variable (except of patch size) that influences the species richness of cavity nesters positively. However, they seem to be negatively influenced by the amount of shrubs. In contrast, *Mörtberg (2001)* found a positive effect of dense shurb layer on the cavity nesting marsh tit *(Parus palustris)*. I suggest that my result might be a consequence of vegetation characteristics correlations rather than a direct negative effect of shrubs on these species. These species tend to positively correlated with the proportion of older trees that potentially offer a good supply of cavities. The oldest trees are typically retained in central parks, but at the same time shrubs are largely removed from such areas. These confusing patterns encourage the consideration of vegetation age composition and its important role in bird assemblage determination. Besides, it has been reported that older stands are preferred by sensitive and also endangered bird species *(Natuhara & Imai 1999; Donnelly 2002; Mörtberg and Wallentinus 2000)*.

Two species groups were responding positively to the growing proportion of herb cover. The omnivorous guild, encompassing corvids and pheasant *(Phasianus colchicus)* feeding mainly on the ground possibly benefit from higher foraging substrate availability. The explanation for long distance migrants is not so straightforward. However, many of long distance migrants are ground nesters and additionally, the herbcover is negatively correlated with the proportion of built-up area. These factors taken together may result in the revealed positive relationship of long distance migrants species diversity and proportion of herb cover, whereas the real response regards the urbanization intensity. The finding that the amount of developed area is a very important and negatively acting factor for long distance migrants in Canada *(Friesen et al. 1995)* provides some support for my hypothesis.

A completely unexpected outcome has been found for the granivorous species guild in this study, where the negative influence of herb layer has been revealed. Although *Mörtberg (2001)* discovered a similar negative relationship, but she studied species that were associated with coniferous forests, where naturally sparse vegetation grows in the herb layer. In contrast, *Emlen (1974)* specifically describes the benefits of granivores in Tucson, in Arizona, because of lawns and weeds producing large amounts of seeds. Looking for explanation of my results regarding the negative effect of herb cover on the granivores, it is important to consider the individuality of species analyzed, many of which are positively reacting to urbanization (such as *Columba palumbus, Streptopelia decaocto, Passer spp., etc.*). I suggest that the confusion arises from the fact that the areas covered by buildings and herbs are negatively correlated, as described above. These species are thus probably reacting to urbanization intensity rather than to the decreasing herb cover.

The presence of water resources increases the species richness of several guilds, the insectivorous guild being one of them. Also species requiring shrubs as nesting substrate are positively associated with water bodies. This association is hypothetically attributable to the fact, that the shrubs are growing densely along the banks of various water bodies, and are not so readily removed as elsewhere within the city. Moreover, water bodies pose some kind of protection from potentially disturbing factors, such as the presence of pedestrians, car traffic and noise *(Fernández-Juricic and Jokimäki 2001).*

My primary aim was to determine the habitat characteristics influencing the bird community at the very local level, besides the patch size and urbanization intensity. The results of multivariate analyses accounting for the effect of overall patch size and distance to the city margin revealed a relatively small effect of other explanatory variables. Nevertheless, this is expectable, due to the large and general effect of the patch size (e.g. *Gavareski 1976; Tilghman 1987; Jokimäki 1999; Mörtberg 2001)* and urbanization pressure (e.g. *Hohtola 1978; McKinney and Lockwood 1999; Clergeau et al. 2006; Evans et al. 2009)* on bird species richness in towns. I suppose that my results provide valuable information that can be employed for local management actions. I corroborated the positive effect of the overall patch size thus I suggest the restriction of further urban encroachment into remnant green patches. Since more species tend to occur in peripheral patches, provision of greenways towards central patches might be favourable for potential colonizers *(Fernández-Juricic 2004).* The herbcover, the tree species richness and the presence of water body exerted significant effects. The effect of the herb cover, considered positive *(Emlen 1974; Willson 1974)*, is in opposition with the effect of buildings, which affect positively only several, and mainly common species (*e.g. Streptopelia decaocto, Pica Pica, Passer spp.*). It is thus desirable to retain as much herb and natural vegetation cover as possible and to avoid unnecessary paving. It is also advisable to increase or at least retain the tree species diversity, but in favour of native tree species. Creating or retaining mosaics of coniferous and deciduous trees may provide habitats favourable for specialist species associated with both of these tree types and thus enrich the urban bird community. Both older and younger tree stands have to be present to support a richer bird community *(Donnelly 2002)*, however more sensitive species tend to be associated with older stands, which may be scarcer in heavily managed urban areas. Therefore I suggest the management practices to be guided towards older stands in cities, since I do not suppose that young stands could become rare in the dynamic urban environment with numerous disturbances. Moreover, the negative effect of the overall small size of forest remnants or parks in central parts of Prague might be partly compensated by the older tree layer. Dead wood should be also retained wherever possible to support a richer food supply for insectivorous birds *(Ehnström 2001)*. I suggest not to remove the shrub undergrowth from older patches as it is often done in Prague, since the positive effect of age structure is impared by unfavourable conditions for birds associted with shrubs. In this respect it is notable, that shrub nesters are forming richer communities near water bodies. The management practices should be restricted along the banks of rivers, streams and ponds where often no interference with human activities occurs. Moreover, the water bodies are a potentially effective barriers reducing the impact of various disturbances. This specific environment is potentially very valuable and deserves more attention.

Besides the need to support the overall species richness of urban bird communities to ensure the contact of city dwellers with nature, it is also necessary to conduct further ecological research to find out more details about the contribution of urban birds to the regional populations.

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Appendix 1. Species list. Occurence = number of points, where a given species was detected; Occurence (%) = proportion of points from the total of 293, where a given species was detected (light grey = species considered in analyses)

Abbreviation	**Scientific name**	**Occurence**	**Occurence (%)**
PhaCol	Phasianus colchicus	51	17.41
ColLiv	Columba livia		
ColPal	Columba palumbus	202	68.94
StrDec	Streptopelia decaocto	61	20.82
CucCan	Cuculus canorus		
ApuApu	Apus apus		
DryMar	Dryocopus martius		
PicVir	Picus viridis	56	19.11
DenMaj	Dendrocopos major	148	50.51
DenMed	Dendrocopos medius	4	1.37
TroTro	Troglodytes troglodytes	51	17.41
HirRus	Hirundo rustica		
DelUrb	Delichon urbica		
MotAlb	Motacilla alba		
PruMod	Prunella modularis	16	5.46
EriRub	Erithacus rubecula	157	53.58
LusMeg	Luscinia megarhynchos	15	5.12
PhoPho	Phoenicurus phoenicurus	61	20.82
PhoOch	Phoenicurus ochruros		
TurVis	Turdus viscivorus		
TurPhi	Turdus philomelos	96	32.76
TurMer	Turdus merula	281	95.9
SylBor	Sylvia borin	33	11.26
SylAtr	Sylvia atricapilla	274	93.52
SylCur	Sylvia curruca	25	8.53
SylCom	Sylvia communis	5	1.71
LocFlu	Locustella fluviatilis		
HipIct	Hippolais icterina		
PhyTro	Phylloscopus trochilus	44	15.02
PhySib	Phylloscopus sibilatrix	48	16.38
PhyCol	Phylloscopus collybita	222	75.77
RegReg	Regulus regulus	11	3.75
RegIgn	Regulus ignicapillus		
MusStr	Muscicapa striata	6	2.05
FicHyp	Ficedula hypoleuca	6	2.05

FicAlb	Ficedula albicollis	30	10.24
ParMaj	Parus major	288	98.29
ParAte	Parus ater	24	8.19
ParCae	Parus caeruleus	279	95.22
ParCri	Parus cristatus		
ParMon	Parus montanus		
ParPal	Parus palustris		
AegCau	Aegithalos caudatus	52	17.75
SitEur	Sitta europea	167	57
CerFam	Certhia familiaris	65	22.18
CerBra	Certhia brachydactyla	15	5.12
OriOri	Oriolus oriolus		
GarGla	Garrulus glandarius	174	59.39
PicPic	Pica pica	104	35.49
CorMon	Corvus monedula	22	7.51
CorFru	Corvus frugilegus	8	2.73
CorCor	Corvus corone		
StuVul	Sturnus vulgaris	44	15.02
PasDom	Passer domesticus	10	3.41
PasMon	Passer montanus	9	3.07
FriCoe	Fringilla coelebs	239	81.57
CarCar	Carduelis carduelis		
CarChl	Carduelis chloris	84	28.67
SerSer	Serinus serinus		
CocCoc	Coccothraustes coccothraustes	26	8.87
EmbCit	Emberiza citrinella	11	3.75

Appendix 2. Species guilds

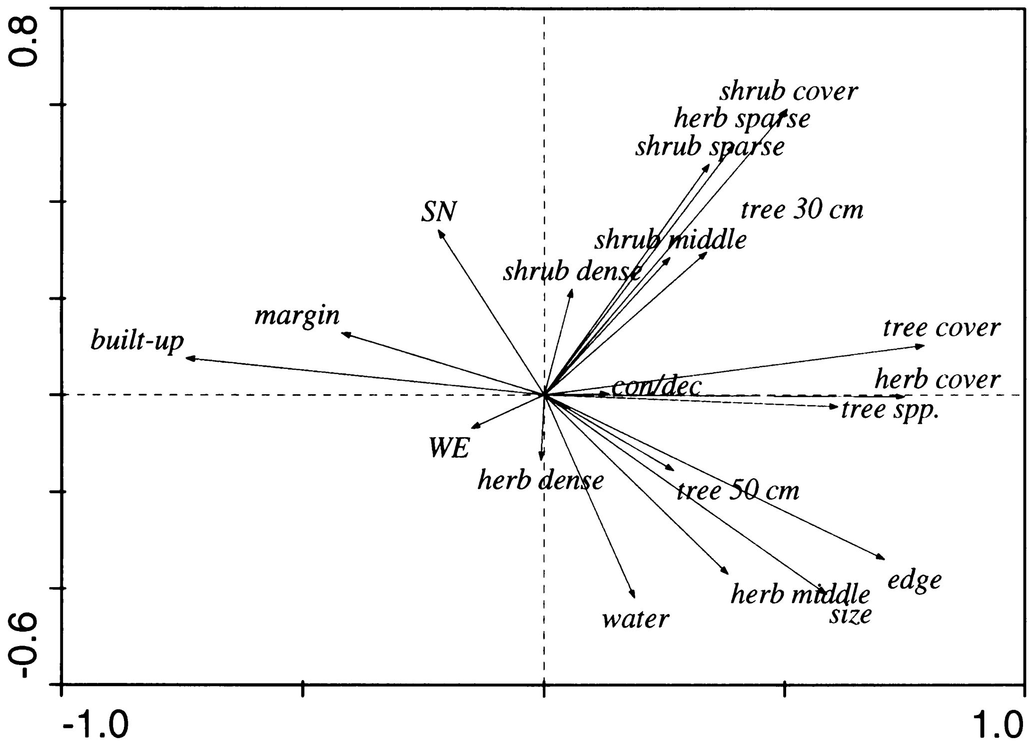
Nesting substrate				
tree	**shrub**	**cavity**	**ground**	**buildings**
ColPal	TroTro	PicVir	EriRub	ColLiv
StrDec	PruMod	DryMar	PhyTro	PhoOch
TurPhi	TurPhi	DenMaj	PhySib	StrDec
TurMer	TurMer	DenMed	PhyCol	MusStr
TurVis	SylBor	PhoPho	PhaCol	PasDom
RegReg	SylAtr	FicAlb	EmbCit	PasMon
MusStr	SylCur	FicHyp	LocFlu	
AegCau	SylCom	ParMaj	LusMeg	
CerBra	HipIct	ParAte		
CerFam	CarChl	ParCae		
PicPic	SerSer	ParMon		
GarGla		ParPal		
FriCoe		SitEur		
CorFru		StuVul		
CorCor		PasMon		
CarCar		CorMon		
SerSer				
CocCoc				
OriOri				

Feeding guild		
granivorous	**insectivorous**	**omnivorous**
ColLiv	PicVir	PicPic
ColPal	DryMar	GarGla
StrDec	DenMed	CorMon
CarCar	DenMaj	CorFru
CarChl	TroTro	CorCor
SerSer	PruMod	PhaCol
CocCoc	EriRub	
PasDom	LusMeg	
PasMon	PhoPho	
FriCoe	PhoOch	
EmbCit	TurPhi	
	TurMer	
	TurVis	
	SylBor	
	SylAtr	
	SylCom	
	SylCur	
	HipIct	
	PhyTro	
	PhySib	
	PhyCol	
	RegReg	
	FicAlb	
	FicHyp	
	MusStr	
	AegCau	
	CerBra	
	CerFam	
	CucCan	
	LocFlu	
	ParMaj	
	ParAte	
	ParCae	
	ParMon	
	ParPal	
	SitEur	
	OriOri	
	StuVul	

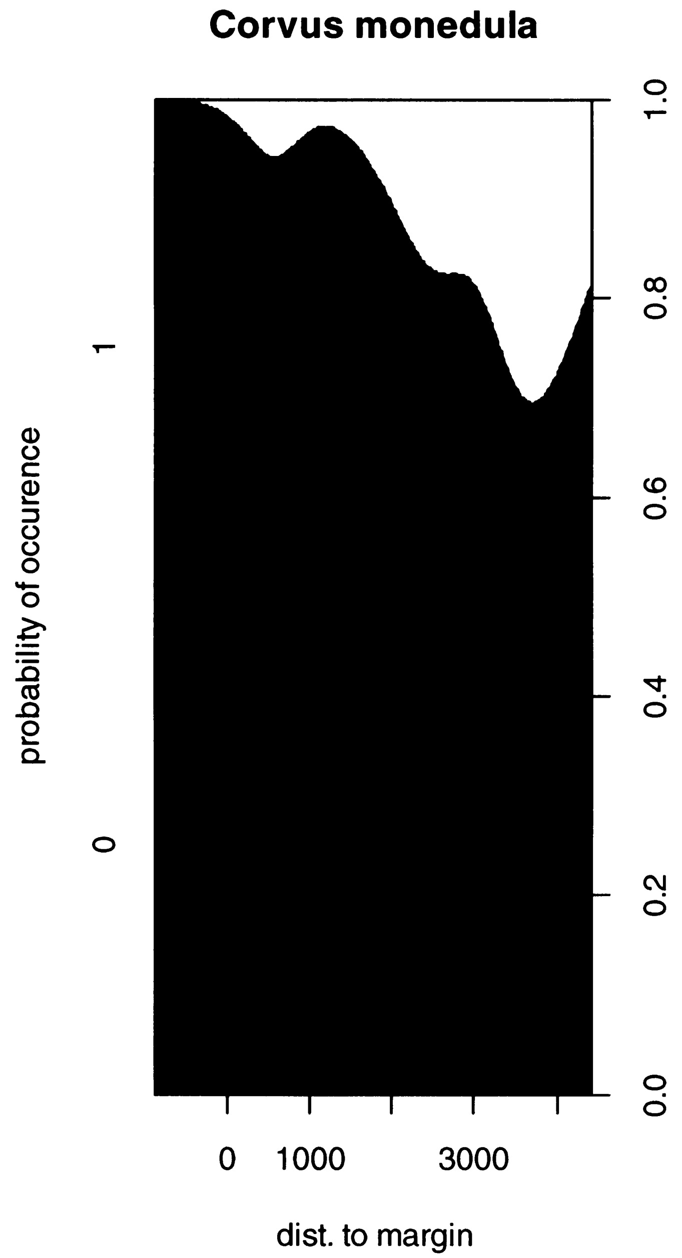
Habitat specialization	
generalist	**specialist**
DenMaj	ColPal
TroTro	PicVir
PruMod	DenMed
EriRub	DryMar
LusMeg	TurVis
PhoPho	PhySib
TurMer	RegReg
TurPhi	MusStr
HipIct	FicHyp
SylBor	FicAlb
SylAtr	ParMon
PhyCol	ParPal
PhyTro	ParAte
AegCau	SitEur
ParCae	CerFam
ParMaj	CerBra
FriCoe	CocCoc
OriOri	GarGla
StuVul	
CorMon	

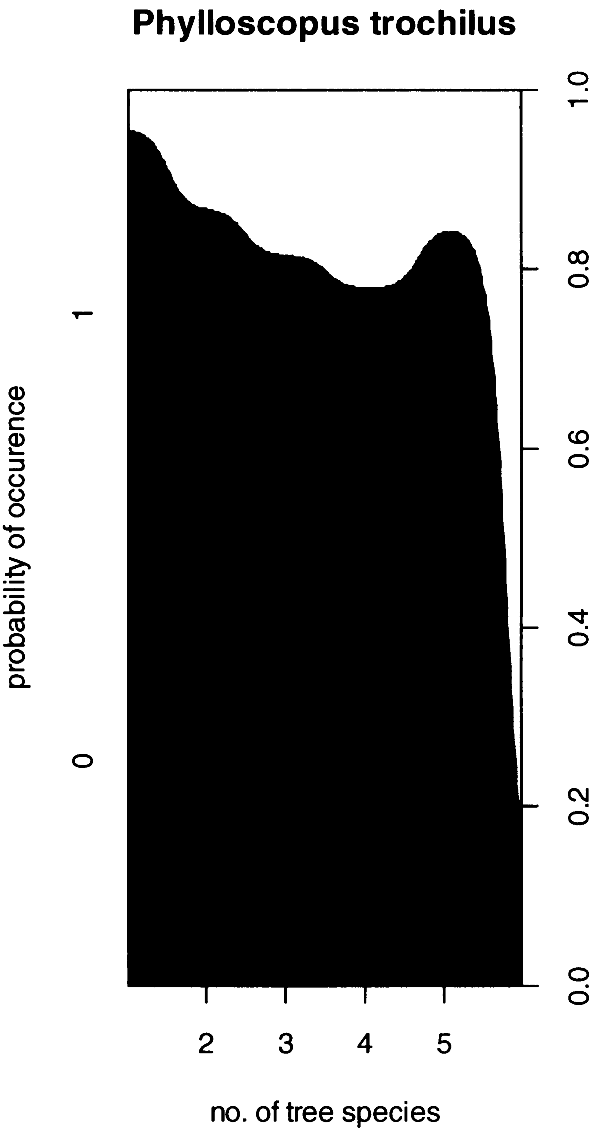
Migration status		
long dist.migr	**short dist.migr**	**non-migr.**
PhoPho	ColPal	ColLiv
LusMeg	TroTro	StrDec
SylBor	PruMod	PicVir
SylAtr	SylAtr	DryMar
SylCom	EriRub	DenMaj
SylCur	PhoOch	DenMed
HipIct	TurPhi	TurMer
PhyTro	TurVis	RegReg
PhySib	PhyCol	ParMaj
PhyCol	StuVul	ParAte
FicAlb	FriCoe	ParCae
FicHyp	CorFru	AegCau
MusStr	CarCar	ParMon
CucCan	SerSer	ParPal
LocFlu	CocCoc	SitEur
OriOri		CerBra
		CerFam
		PicPic
		GarGla
		StuVul
		PasDom
		PasMon
		CorMon
		CorCor
		CarChl
		CarCar
		EmbCit
		PhaCol

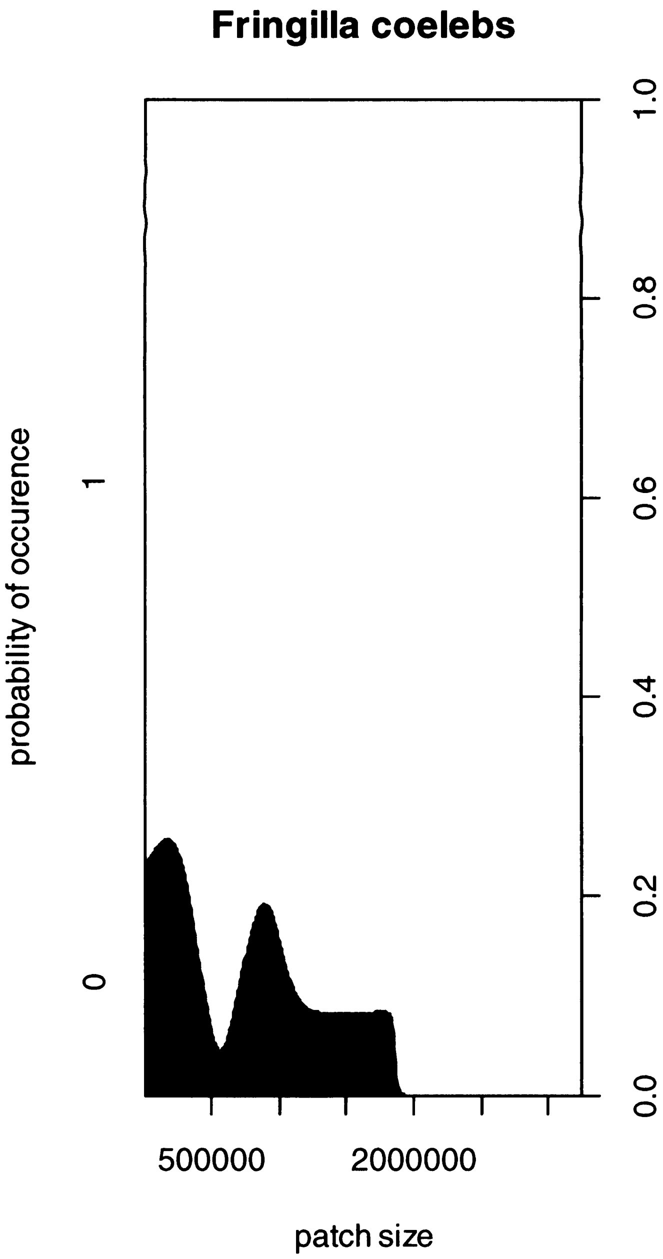
Appendix 3. Principal Component Analysis describing the correlations among explanatory variables (used as „species“ in analysis).



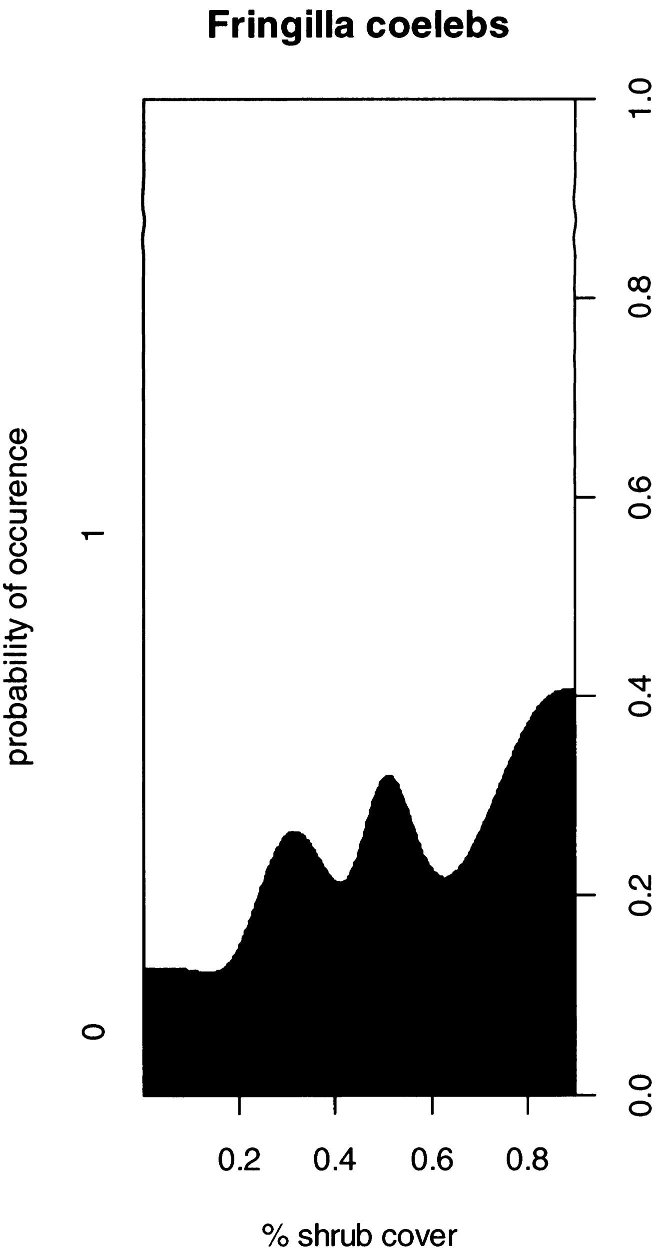
Appendix 4. Occurrence probability plots of four selected species. x-axis: significant explanatory variable ($p < 0.05$); y-axis probability of occurrence (lighter grey = higher probability of occurrence).



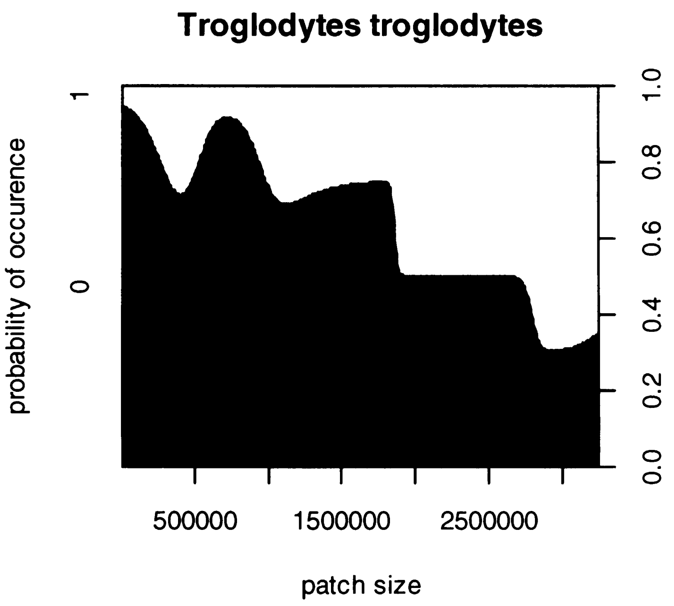

Phylloscopus trochilus
probability of occurence
0
1
0.0
0.2
0.4
0.6
0.8
1.0
2
3
4
5
no. of tree species



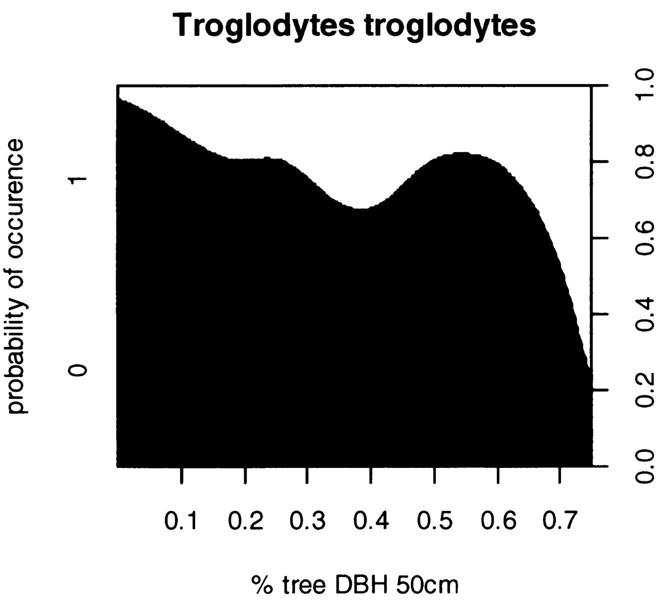
Fringilla coelebs



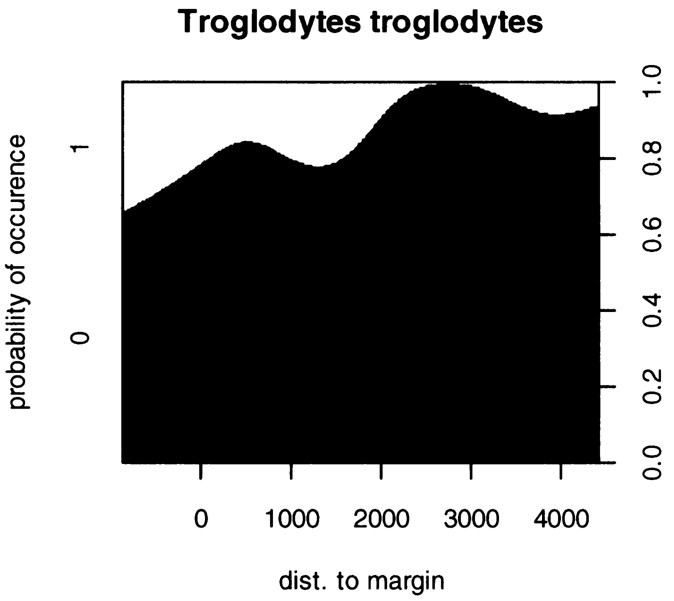
Fringilla coelebs



Troglodytes troglodytes



Troglodytes troglodytes



Troglodytes troglodytes