Biodiversity in urban landscape matrices: from species richness to functional community structure

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Thomas Sattler

von Riedholz

Leiter der Arbeit:

Prof. Dr. R. Arlettaz
Institute of Ecology and Evolution, University of Bern

Dr. F. Bontadina
Institute of Ecology and Evolution, University of Bern

Prof. Dr. P. Duelli
Swiss Federal Research Institute WSL, Birmensdorf

Dr. M. Moretti
Swiss Federal Research Institute WSL, Bellinzona

Dr. M. K. Obrist
Swiss Federal Research Institute WSL, Birmensdorf

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Von der Philosophisch-naturwissenschaftlichen Fakultät
angenommen.

Bern, 22. September 2009

Der Dekan
Prof. Dr. U. Feller

Contents

1

General Introduction

1.1 Increasing importance of cities

'The battle for sustainable development will be won or lost in the urban environment'. With this provocative statement, Klaus Toepfer, the former director of the United Nations Environment Programme (UNEP), opened the meeting of the UN Habitat Governing Council in April 2005. He was drawing on several issues related to the dimension and importance of urban areas: 1) the increasing population numbers of people living in cities worldwide; 2) the energy (incl. food) consumption by the urban population creating an ecological footprint 500-1000 times as large as the actually populated area (Rees 2001); 3) the growing land consumption of sprawling cities endangering natural ecosystems on the one hand but creating new habitat types on the other hand; 4) the political weight of the public opinion regarding environmental and conservation issues of the urban population. In the frame of the introduction to my PhD on urban biodiversity, I can, of course, not discuss all these issues mentioned, but I would like to give an overview on the issues that are relevant for the research I performed together with the support of many additional people in the last three and a half years.

1.1.1 Urban population

Nowadays, more than half of the world's human population lives in cities (United Nations 2008). Population projections predict that the population living in urban areas is set to increase from 3.3 billion in 2007 to 6.4 billion in 2050. In more developed regions of the world, the proportion of the inhabitants living in urban areas is expected to rise from 74% in 2007 to 86% in 2050, while in the less developed regions the same figure increases from 44% to 67% over the same time period (world mean 70% in 2050). In Switzerland, the urban population consisted of 36.0% in 1930, 61.5% in 1980 and 73.4% in the year 2000 (Schuler et al. 2004). Considering these figures, it is no surprise that urban areas are one of the fastest growing habitat types worldwide. Currently, cities occupy less than 3% of the global terrestrial surface (Grimm et al. 2008). On a global scale, the land mass covered by cities may seem small; in some European regions, however, this proportion is substantial. In the United Kingdom, nearly 10% of the land area is considered to be urbanized (Fuller et al. 2002), while in Switzerland, the extent of human settlements covers 7%. This fraction rises to 15% in the Swiss Plains since large areas of the Alps are unsuitable for settlement (Federal Office for Spatial Development 2005, Swiss Federal Statistical Office 2005).

1.1.2 Processes in cities: expansion and densification

The ever increasing population in cities and the rising demands on living space – the average Swiss resident used 97m^2 in 1982 and 112 in 1995 m^2 (Swiss Federal Statistical Office 2005) – generates two different processes in urban areas: expansion of cities ('urban sprawl') and densification of the already built area (Fig. 1). Expansion of urban areas has been recognised as a serious issue by the general public in Switzerland while densification is less of a topic. According to a representative survey on behalf of a large Swiss NGO, 55% of the Swiss population expressed the opinion that too much land is built-up in Switzerland. Swiss citizens will vote on an initiative aimed at limiting land use by buildings. The Federal Office for Spatial Development (ARE) has set itself the long-term goal of limiting total settlement space (buildings, gardens and roads) to 400m^2 per person. These intentions will essentially increase the pressure on the remaining non-built-up areas within Swiss cities. The resulting densification in turn will affect habitat availability for urban biodiversity.

1.2 Biodiversity

1.2.1 The signification of 'biodiversity'

Most natural scientists refer to the convention on Biological Diversity (United Nations 1992) when defining the broad term 'biodiversity': biodiversity means species, genetic and landscape diversity. With this approach, scientists often neglect the fact that the broad public, including authorities and politicians, usually does not refer to these concepts when using the term. Often people mean 'nature in general' (Home et al. in

Press), emblematic and/or endangered individual species (Duelli et al. 2005) or possibly 'many species' in the sense of high species numbers (Obrist and Duelli submitted). As we will see below, the different value systems of humans need to be considered when evaluating 'biodiversity' in a concept that is meaningful to society. Despite this criticism, the importance of the convention on Biological Diversity is unrivalled, and proved to be successful in both science and society. On the European political agenda, a topical issue is, for instance, the goal of halting the loss of biodiversity by 2010 ('Countdown 2010'). In recent years, the term biodiversity has even become a quality label in landscape evaluation (Duelli 2006). Conservation, maintenance and enhancement of biodiversity are considered to be of vital importance for ecological sustainability in cultivated landscapes and for human recreation in tourist regions.

For the general public, species diversity is the readily recognisable form of biodiversity (Myers et al. 2000). Species are the currency for 'biodiversity' that are most appealing to people. This is an important fact which I considered for my research approach. However, it must also be considered that many people do not know its significance: a representative survey in 2005 showed that 52% of Swiss inhabitants are unfamiliar with this expression, and for many people the term 'biodiversity' means the same as 'nature' (Home et al. submitted).

1.2.2 Biodiversity and value systems

It has become increasingly evident that the perception and the personal concept of biodiversity very much depends on the motivations and value systems of the individual person (Duelli et al. 2007). Anthropocentric value systems for biodiversity include conservation of species, conservation of habitats, ecological stability ('balance of nature'), ecosystem services (e.g. pollination, pest control), wilderness, uniqueness and cultural heritage.

For urban inhabitants, some aspects of urban biodiversity are more relevant than others. What are the potential motivational drivers for protecting or enhancing biodiversity in urban environments? The benefits of biodiversity can be split into 3 value systems: non-use, direct-use and indirect-use values (Gaston and Spicer 2004). The non-use values are based on ethical motivations, and the values behind it are called intrinsic, existence, option or bequest values. These values are a potentially strong motivation for the conservation of biodiversity in cities, but people usually think of wild, untouched biodiversity outside cities when considering these motivations. In urban areas, there are only few direct-use values of biodiversity; people rarely obtain direct profit from biodiversity trough food, medicinal or industrial products, or pest control. Income generated by visitors to zoos and botanical gardens can be considered as a direct-use value of biodiversity in cities. However, by far the strongest, but also least conscious, motivation for the conservation of biodiversity in cities are recreational benefits (regeneration from mental fatigue), which I consider to be indirect use values. Every day millions of people, consciously or unconsciously, seek this benefit through biodiversity in urban parks, along water edges or in forests close to cities. The importance of nature in urban environments has been the focus of social and psychological studies and it has been found that easily accessible urban green spaces provide a necessary substitute for contact with nature on a larger scale (Peron et al. 2002, Hernandez and Hidalgo 2005, Fuller et al. 2007, Home 2007, Home et al. in Press). Contact with diverse nature plays an important role for perceived quality of life (Miller 2006). Additional indirect-use values of biodiversity, such as ecological resilience and environmental ecosystem services, might be most important in natural, agricultural and forested landscapes, but of course they are also, to some extent, relevant in urban areas (heat absorption, emission reduction). People living in cities draw on ecosystem services from areas at least 500-1000 times larger than the areas of the cities themselves (Folke et al. 1997). The higher the ecosystem services within cities, the smaller is the 'ecological footprint' (Rees 2001) of the city dwellers outside the cities. Despite all these benefits of urban biodiversity, one has to remember that most urban people consciously perceive and enjoy biodiversity in non-urban areas, e.g. during holidays abroad, while the values of urban biodiversity are largely ignored.

1.2.3 Urban biodiversity

Urban areas had long been disregarded as study objects in ecological research. The belated recognition that urban areas can form important habitats for plants and animals has led to a remarkable increase in the number of studies in settled areas, particularly over the last 15 years (McDonnell and Hahs 2008). This rise in the number of studies reflects the growing importance of cities worldwide.

Urbanisation represents a far-reaching human impact on the environment and has led to a dramatic transformation of landscapes (Vitousek et al. 1997, Liu et al. 2003). Despite the high human impact, urban areas still function as ecosystems and contain the same processes (energy, nutrient, water cycles) and components (plants, animals, water, soil, etc.) as less densely populated areas (Sukopp and Wittig 1998, Zipperer et al. 2000, McDonnell et al. 2009). Urban ecosystems give rise to new habitat types such as gardens, parks and green roofs. They provide opportunities for populations of numerous plant and animal species, which might even be more abundant in urban areas than in other ostensibly 'natural' areas (Marzluff 2001, McKinney 2002, Thompson et al. 2004, Angold et al. 2006, Smith et al. 2006). The warmer climate in cities, known as the heat island effect (Pickett et al. 2001), thereby plays an important role, e.g. in shaping dry and warm habitats.

Many studies on urban biodiversity have compared urban with non-urban areas (e.g. on a rural – urban gradient (McDonnell and Pickett 1990, McDonnell and Hahs 2008) or in remnants of natural habitats (e.g. Gibb and Hochuli 2002, Shochat et al. 2004, Bolger et al. 2008)). Despite the acquired knowledge in urban ecology, there is an urgent need to identify the important variables (environmental, social) and their respective effect sizes, which shape biodiversity within urban areas (Brunzel et al. 2009).

1.2.4 Including the social dimension in urban ecology

In recent years, urban ecological research has come to recognise that any research performed in an urban area needs to consider the social dimension in the system. Only in this way can the development of more sustainable cities be possible (Grimm et al. 2008, Wu 2008, McDonnell et al. 2009). Social sciences as well realise that the increasing urbanisation of most people's surroundings tremendously affects their quality of life (Home 2007, Home et al. in Press) and that ecological knowledge must be improved and better integrated into social science research and ultimately into urban planning (Breuste et al. 2008). Most people's appreciation of biodiversity takes place within the boundaries of a city. It is necessary that people experience the benefits of a diverse biodiversity in these surroundings, e.g. through an improved quality of life. Thanks to such positive experiences, city residents may be ready to revise their (possibly absent or negative) attitudes and opinions towards biodiversity (Hunter and Rinner 2004). Such a process of emotional realisation might affect decisions regarding biodiversity, or environmental and sustainable issues in general. By their sheer mass, the opinions of urban residents will influence political decisions on biodiversity conservation outside cities (e.g. wolf recolonisation in Switzerland is generally welcomed by city residents but regarded negatively by the rural populace). Thus, some authors state that the wealth of experience of urban biodiversity will crucially influence nature conservation worldwide (Dunn et al. 2006).

1.3 Interdisciplinary research project ‘BiodiverCity’

My PhD project formed part of the interdisciplinary project ‘BiodiverCity’ (www.biodivercity.ch). BiodiverCity aims at the identification, maintenance and enhancement of biodiversity and its acceptance in the urban development process. BiodiverCity was funded by the Swiss National Science Foundation as a project of the National Research Program 54 ‘Sustainable development of the built environment’ (www.nrp54.ch). The scope of the overarching BiodiverCity project had great impact on the questions and on the study systems of my PhD. BiodiverCity is split into two research modules: the social science module (PhD Robert Home) is interested in the perceptions of biodiversity and the corresponding human value systems of the city inhabitants. The scope and parts of the ecological module are elucidated in greater detail below.

1.4 Research approach

The ecological module of BiodiverCity (and thus my PhD) focuses on biodiversity aspects which are of relevance for city residents. As outlined above, species diversity is the readily recognisable form of biodiversity for the general public (Myers et al. 2000). I chose a broad approach to species diversity, including a variety of taxonomical groups and analysing several aspects of this term. Thereby I consider a high species biodiversity as a quality of nature that improves the perceived life quality of city inhabitants.

Throughout the chapters, I move from broad to specific species diversity, meaning from the generalising 'total species richness' (Alpha diversity; chapters 2 & 3) and species richness of functional groups (2) to species composition (communities, Beta diversity; chapter 4) to single species (chapters 5-7).

1.4.1 Introduction to chapters

Fig. 2 gives an overview on sampling design, taxonomical groups considered and the analysis performed in the present PhD project.

Chapter 2: Arthropods comprise up to 65% of all multicellular species (Hammond 1992), occupy diverse trophic levels and are fundamental for the functioning of ecosystems. Thus, this taxonomic group is a good subject matter for studying species richness and the richness of five functional groups (zoophagous, phytophagous, pollinator, low mobility, and high mobility species). By doing so, we also obtain a surrogate measure for ecological resilience. We predict the effect sizes of five urban gradients on the species richness of all six groups. These five gradients are the age of the urban settlement, the proportions of impervious area, habitat management, and the configuration and composition of the urban mosaic.

Chapter 3: Vertebrate species such as birds (Aves) are appealing to people. They are highly visible, attractive, and their ecology is well known.

Species richness and a diversity index (Simpson index) are analysed with respect to structural elements, the composition of the urban Green (coniferous/deciduous, native/exotic) and the influence of short- and long-term green management. We predict their respective effect sizes on both measures of urban bird diversity.

Chapter 4: Distributions of species in general and of communities in particular are spatially organized (Wiens 1989, Fortin and Dale 2005). It is thus important to consider spatial structure of the species and their composition in order to understand ecological patterns (Legendre 1993, Koenig 1999). However, spatial analysis of species communities in urban areas has rarely been performed. In this chapter I analyse the relative contribution of autogenous (biotic) processes (i.e. dispersal, growth, mortality, interspecific competition) and exogenous processes (species respond to environmental variables that themselves are spatially structured) to explain the spatial structure of spider (Araneae), bee (Apidae) and bird (Aves) communities in cities.

Chapter 5: Despite their elusive nocturnal lifestyle, bats (Chiroptera) enjoy a high level of societal appreciation – their urban ecology, however, is rather unknown. Due to their social organisation in roosts, the distribution of foraging bats in space is expected to be spatially aggregated. I analyse the relative contribution of environmental, spatial and food variables explaining activity variation in six different bat species.

Chapter 6: The phytophagous group of weevils (Curculionoidea) represents a species-rich coleopteran group. Recently, non-systematic surveys in urban areas have yielded seven species that are new to the Swiss fauna. Thanks to a systematic sampling, this chapter provides baseline information regarding species identities, steadiness and dominance in the weevil fauna in Swiss cities.

Chapter 7: Due to sample bias, systematic surveys of arthropods regularly yield rare species, including new species to countries. The incompleteness of species inventories are aggravated in cities which are avoided by naturalists. Using the example of five wild bee species (Apidae), we discuss the question of whether these species are recent immigrants or whether they have so far been overlooked.

Chapter 8: In this chapter, we summarise the important findings and conclude on both scientific and practical implications of this study.

1.5 References

Angold, P. G., J. P. Sadler, M. O. Hill, A. Pullin, S. Rushton, K. Austin, E. Small, B. Wood, R. Wadsworth, R. Sanderson, and K. Thompson. 2006. Biodiversity in urban habitat patches. Science of the Total Environment 360:196-204.

Bolger, D. T., K. H. Beard, A. V. Suarez, and T. J. Case. 2008. Increased abundance of native and non-native spiders with habitat fragmentation. Diversity and Distributions 14:655-665.

Breuste, J., J. Niemela, and R. P. H. Snep. 2008. Applying landscape ecological principles in urban environments. Landscape Ecology 23:1139-1142.

Brunzel, S., S. F. Fischer, J. Schneider, J. Jetzkowitz, and R. Brandl. 2009. Neo- and archaeophytes respond more strongly than natives to socio-economic mobility and disturbance patterns along an urban-rural gradient. Journal of Biogeography 36:835-844.

Duelli, P. 2006. Biodiversität als Landschaftsqualität. Page 319 in T. K.M., M. Bürgi, and T. Coch, editors. Landschaftsqualitäten – Festschrift zur Emeritierung von Prof. Dr. K.C. Ewald. Haupt, Bern.

Duelli, P., P. Baur, M. Buchecker, F. Gugerli, R. Holderegger, and T. Wohlgemuth. 2007. The role of value systems in landscape research. Pages 27-34 in F. Kienast, S. Ghosh, and O. Wildi, editors. A changing world: challenges for landscape research. Springer Landscape Series, Dordrecht, NL.

Duelli, P., V. Chumak, M. K. Obrist, and P. Wirz. 2005. The biodiversity values of European virgin forests. Forest Snow and Landscape Research 79:91-99.

Dunn, R. R., M. C. Gavin, M. C. Sanchez, and J. N. Solomon. 2006. The pigeon paradox: Dependence of global conservation on urban nature. Conservation Biology 20:1814-1816.

Federal Office for Spatial Development. 2005. Raumentwicklungsbericht 2005. Eidg. Departement für Umwelt, Verkehr, Energie und Kommunikation (UVEK), Bern.

Folke, C, Å. Jansson, J. Larsson, and R. Constanza. 1997. Ecosystem appropriation of cities. Ambio 26:167-172.

Fortin, D. and M. R. T. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3:390-394.

Fuller, R. M., G. M. Smith, J. M. Sanderson, R. A. Hill, A. G. Thomson, R. Cox, N. J. Brown, R. T. Clarke, P. Rothery, and F. F. Gerard. 2002. Countryside Survey 2000 Module 7. Land Cover Map 2000. Final Report CSLCM. Centre for Ecology and Hydrology, Monks Wood, UK.

Gaston, K. J. and J. I. Spicer. 2004. Biodiversity: An Introduction. Blackwell Publishing, Malden, Massachusetts.

Gibb, H, and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106:91-100.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. G. Wu, X. M. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. Science 319:756-760.

Hammond, P. M. 1992. Species inventory. Pages 17-39 in B. Groombridge, editor. Global Biodiversity, Status of the Earth Living Ressources. Chapman and Hall, London.

Hernandez, B. and M. C. Hidalgo. 2005. Effect of Urban Vegetation on Psychological Restorativeness. Psychological reports 96:1025-1028.

Home, R., N. Bauer, and M. Hunziker. in Press. Cultural and Biological Determinants in the Evaluation of Urban Green Spaces. Environment and Behavior.

Home, R., N. Bauer, and M. Hunziker. submitted. Psychosocial Outcomes as Motivations for Visiting Nearby Green Spaces. Leisure Sciences.

Home, R., Bauer, N. & Hunziker, M. 2007. Constructing Urban Greenspaces: An Application of Kelly's Repertory Grid. Tourism Review 62:47-52.

Hunter, L., and L. Rinner. 2004. The association between environmental perspective and knowledge and concern with species diversity. Society and Natural Resources 17:517-532.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution 14:22-26.

Legendre, P. 1993. Spatial Autocorrelation – Trouble or New Paradigm. Ecology 74:1659-1673.

Liu, J., G. C. Daily, P. R. Ehrlich, and G. W. Luck. 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421:530-533.

Marzluff, J. M. 2001. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston.

McDonnell, M. J., J. Breuste, and A. K. Hahs. 2009. Introduction: Scope of the book and need for developing a comparative approach to the ecological study of cities and towns. Pages 1-5 in M. J. McDonnell, A. K. Hahs, and J. Breuste, editors. Ecology of Cities and Towns. A comparative Approach. Cambridge University Press.

McDonnell, M. J. and A. K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23:1143-1155.

McDonnell, M. J. and S. T. A. Pickett. 1990. Ecosystem Structure and Function Along Urban Rural Gradients – an Unexploited Opportunity for Ecology. Ecology 71:1232-1237.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. Bioscience 52:883-890.

Miller, J. 2006. Restoration, reconciliation, and reconnecting with nature nearby. Biological Conservation 127:356-361.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Obrist, M. K. and P. Duelli. submitted. Rapid Biodiversity Assessment (RBA) of arthropods for monitoring average local species richness and related ecosystem services. Biodiversity and Conservation.

Peron, E., R. Berto, and T. Purcell. 2002. Restorativeness, Preference and the Perceived Naturalness of Places. Medio Ambiente y Comportamiento Humano 3:19-34.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.

Rees, W. E. 2001. Ecological footprint, concept of. Pages 229-244 Encyclopedia of Biodiversity. Academic Press, San Diego, CA.

Schuler, M., M. Perlik, and N. Pasche. 2004. Nicht-städtisch, rural oder peripher – wo steht der ländliche Raum heute? ARE, Bundesamt für Raumentwicklung, Bern.

Shochat, E., W. L. Stefanov, M. E. A. Whitehouse, and S. H. Faeth. 2004. Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. Ecological Applications 14:268-280.

Smith, R. M., P. H. Warren, K. Thompson, and K. J. Gaston. 2006. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15:2415-2438.

Sukopp, H. and R. Wittig. 1998. Stadtökologie. 2nd edition. Fischer, Stuttgart

Swiss Federal Statistical Office. 2005. Arealstatistik Schweiz: Zahlen – Fakten – Analysen. Neuchâtel

Thompson, K., J. G. Hodgson, R. M. Smith, P. H. Warren, and K. J. Gaston. 2004. Urban domestic gardens (III): Composition and diversity of lawn floras. Journal of Vegetation Science 15:373-378.

United Nations. 1992. Convention on Biological Diversity. Concluded at Rio de Janeiro on 5 June 1992.

United Nations. 2008. World Urbanization Prospects: the 2007 Revision. United Nations, New York.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494-499.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wu, J. G. 2008. Making the case for landscape ecology – an effective approach to urban sustainability. Landscape Journal 27:41-50.

Zipperer, W. C., J. G. Wu, R. V. Pouyat, and S. T. A. Pickett. 2000. The application of ecological principles to urban and urbanizing landscapes. Ecological Applications 10:685-688.

1.6 Figures

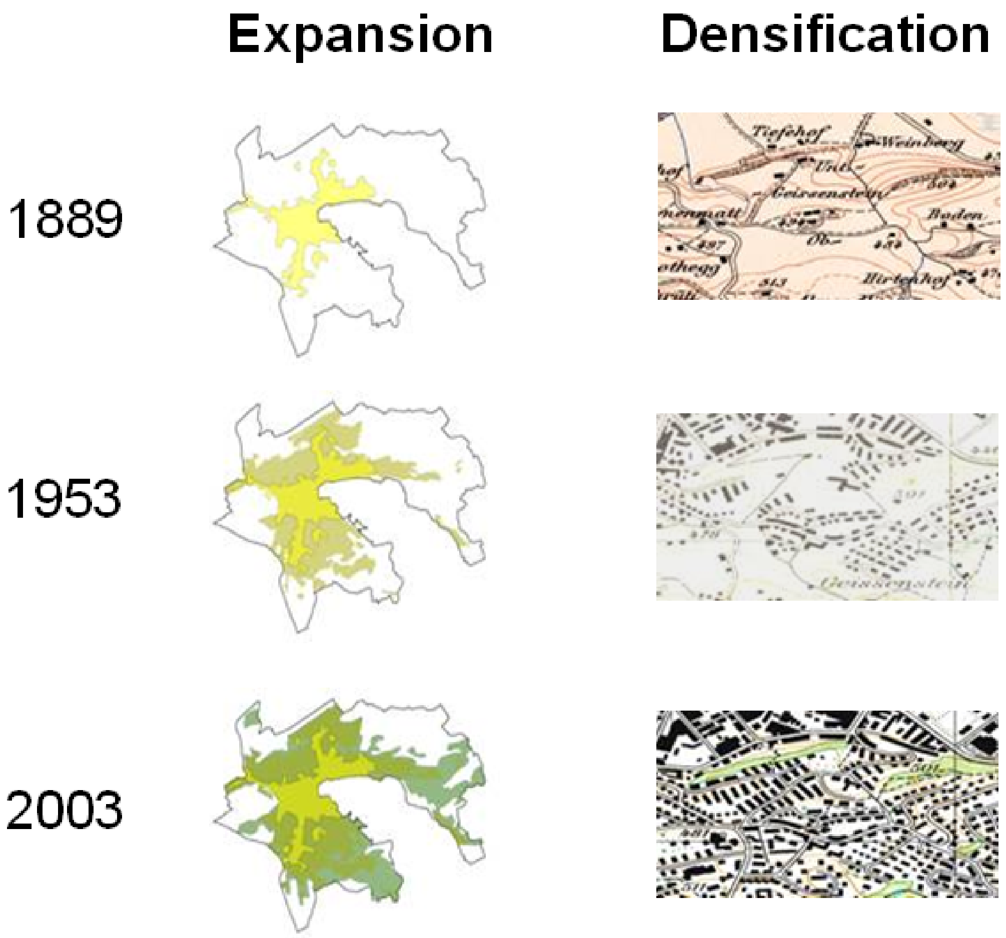

Fig. 1: The urban processes of expansion over time, exemplified by the city of Lucerne (left; city borders as grey lines; yellow: expansion of the urban area in 1889; olive: in 1953; green: in 2003), and densification (right; the same selected perimeter within the city of Lucerne over time).

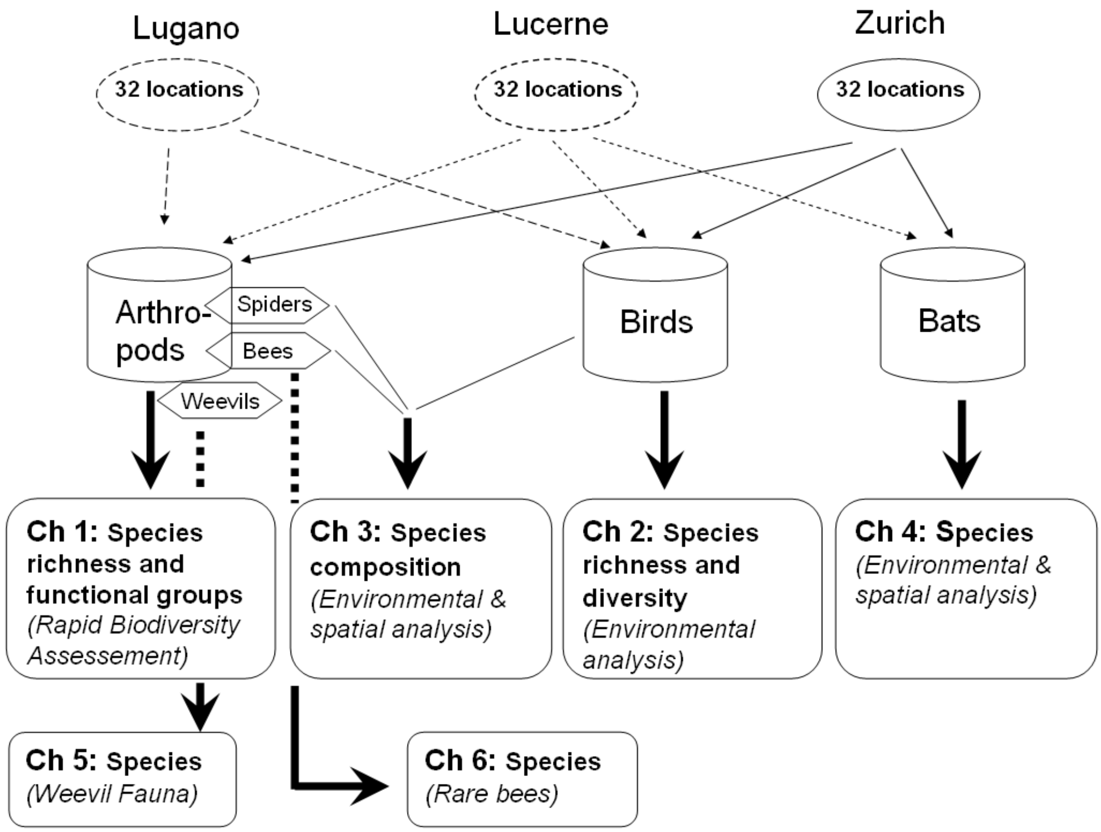

Fig. 2: Overview on sampling design, taxonomical groups considered and the analysis performed in the present PhD project. All taxonomical groups (arthropods, birds and bats) were surveyed at the same sampling locations in three Swiss cities (3 x 32 = 96 locations).

2

Response of arthropod species richness and functional groups to urban habitat structure and management

Response of arthropod species richness and functional groups to urban habitat structure and management

T. Sattler[1, 2], P. Duelli[3], M.K. Obrist[3], R. Arlettaz[2], M. Moretti[1]:

[1] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[2] Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[3] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

In review in *Landscape Ecology*

2.1 Abstract

Urban areas, a worldwide rapidly spreading ecocomplex, represent a particular landscape matrix characterized by fine-grained spatial arrangement of very diverse habitats. We investigated arthropods, which are highly responsive to site-scale environmental patterns, to identify biodiversity-habitat associations along five urban gradients in three Swiss cities (96 study sites), with the aim of identifying species rich urban habitat features. We considered both total species richness and species richness within different functional groups (zoophagous, phytophagous, pollinator, low mobility, and high mobility species). Information theoretical model selection procedures were applied and predictions were calculated based on weighted models. Results show that urban areas host a considerable number of arthropod species (mean: 284, range: 169 – 361), with species richness correlating mostly with indices expressing configuration and composition of the urban mosaic. Species richness also increased with the age of the urban settlement, while enlarged proportions of impervious area and intensified habitat management exerted negative effects. Functional groups showed contrasted, specific responses to environmental variables. Overall, species richness appeared surprisingly robust along the gradients, possibly due to the fine-grained spatial interlinkage of good (heterogeneous) and bad (sealed) habitats. The highly fragmented nature of urban areas may not represent a major obstacle for the arthropods currently existing in cities, because they have probably been selected for tolerance to fragmentation and for high colonisation potential. Given that built areas are increasingly densifying, maintaining if not increasing spatial heterogeneity of the urban green offers potential for counteracting the detrimental effects of progressive sealing upon urban biodiversity. Our results provide some guidance to that endeavour.

Keywords

Rapid Biodiversity Assessment, morphospecies, insects, spiders, ecosystem services, resilience, Switzerland

2.2 Introduction

Recognition of cities as important habitats for plants and animals has led to a recent increase in ecological studies in urban areas (McDonnell and Hahs 2008). This trend reflects the appreciation of ecologists of the growing importance of cities as a study object with particular characteristics. More than half of the human population worldwide lives in cities (United Nations 2008) on less than 3% of the global terrestrial surface (Grimm et al. 2008). This proportion is substantially higher in some European regions with nearly 10% of the United Kingdom (Fuller et al. 2002) and 15% of the Swiss Plain (Bundesamt für Statistik 2005) having become urbanized. Urban areas are among the fastest growing habitat types worldwide and the urban population is predicted to increase from 3.3 billion in 2007 to 6.4 billion in 2050 (United Nations 2008).

Contact with nature contributes to human health (de Vries et al. 2003) and the general human well being (Fuller et al. 2007). For urban residents, first hand experience with wilderness has been replaced by experiences with urban nature (Miller 2005). The opinions of the urban residents influence political decisions on nature conservation outside cities (Dunn et al. 2006), but the opinion of urban residents on nature conservation is mostly based on their urban experience of nature (Hunter and Rinner 2004).

Species diversity has an intrinsic value (Elliot 1992), which per se represents a reason to conserve it. In addition, species richness is considered as a prime indicator for resilience (Duelli and Obrist 2003; Moretti et al. 2006). Ecological resilience reflects the capacity of a ecosystem to maintain structures and functions in the presence of stress (Rapport et al. 1998, Walker et al. 2004). An ecosystem is more resilient when it is species-rich (Bengtsson et al. 2002). For example, a species rich ecosystem is more resistant to invasion, since the available resources are used more efficiently (Loreau et al. 2002). In this sense, species richness is an indicator for resilience and thus for ecosystem health (Rapport et al. 1998; Tzoulas et al. 2007) and a healthy ecosystem provides ecosystem services. Although arthropods deliver several ecosystem services such as pest control and pollination, urban arthropods are seldom split into functional groups when assessing specific ecosystem services (but see Denys and Schmidt 1998; Sanford et al. 2009). Most studies on arthropods in urban areas concentrate on specific groups or aspects of species diversity. Furthermore, most urban studies so far have focused on a rural – suburban – urban gradient (McDonnell and Hahs 2008) and few studies cover a wide taxonomic range (McIntyre et al. 2001; Smith et al. 2006a; Smith et al. 2006b) due to the inherent challenges when investigating such an abundant and species-rich group (McIntyre 2000). To address this difficulty, the Rapid Biodiversity Assessment (RBA) method was established in which arthropod specimens are determined to morphospecies level or as 'recognisable taxonomic units' by entomologically trained non-specialists (Oliver and Beattie 1993). RBA is useful to compare species numbers of locations in similar habitats and it has been shown that the number of morphospecies strongly correlates with total richness of taxonomically determined species (Duelli and Obrist 2005; Obrist and Duelli submitted). If morphospecies are counted according to taxonomical groups that can be attributed to functional levels such as pollinators and zoophagous species, they additionally allow assessment of the potential for ecosystem services.

This study of arthropods in three Swiss cities estimates total species richness and specific ecosystem services (pollination and pest control) by evaluating species richness of functional groups based on their diet (zoophagous, phytophagous species) and function (pollinators). The ability of species of different levels of mobility to colonize suitable habitat patches has implications for the resilience of an ecosystem, especially in heterogeneous landscapes (Loreau et al. 2003) such as urban matrices. Therefore, we also split the species into two mobility classes (low, high). We chose three quantified urban habitat variables 'age of green area', 'human management intensity' and 'fraction of impervious area' to study their influence on species richness. These variables best reflect past and present anthropogenic influences and represent important structural elements in urban areas. Age of the green area combines the effects of stochastic local immigration and increased ecological niches with the succession of the built area. We then contrasted these three urban variables with parameters for fine scale structural heterogeneity, as heterogeneity is an important factor determining arthropod species richness outside urban areas (Duelli 1997; Jonsen and Fahrig 1997; Niemela et al. 1996). In addition, heterogeneity represents the urban mosaic, which is a typical urban characteristic. Finally, heterogeneity is also indicative of the number of ecological niches in that the more heterogeneous an area, the more niches and thus the more species can be expected to be found (Whittaker et al. 2001). Specifically, we ask: A) What influence do the three urban variables 1) age of green area, 2) management intensity of green area and 3) impervious area (sealed and built area) have on arthropod species richness and functional groups? B) What influence has heterogeneity of urban habitats on arthropod species richness and functional groups in comparison to the three urban variables? C) How can different response patterns of functional groups be explained?

2.3 Methods

2.3.1 Study sites and sampling design

Data were collected in the three Swiss cities of Zurich, Lucerne (both North of the Alps) and Lugano (South of the Alps; Supplementary material A), which are representative of small to medium sized cities (Zurich 371’000 inhabitants/92km^2, Lucerne 59’000/24km^2, Lugano 53'000/26km^2) of the central European lowlands (273-436m asl). All cities are composed of historical centres, residential areas including old gardens, parks and cemeteries (all often > 100 years), business quarters and former but discontinued industrial areas, which are rebuilt for new purposes. All three cities border a lake and experience a temperate climate (North: average January temperature 1°C, July 17°C; South: January 3°C, July 20°C).

Within each city, 32 study locations were chosen (total 96) to include all possible combinations of the three gradients age of green area, impervious area, and management. The study locations included private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings (detailed locations in Germann et al. 2008). A minimum distance of 250m was kept between study locations and towards city margins, thereby avoiding spatial auto-correlation of variables (tested with Moran's Index; Legendre and Legendre 1998).

2.3.2 Arthropod sampling and determination of species numbers

Here, we indicate the general procedure of RBA. Methodological details and minor modifications to the original method are specified in Supplementary material B. We applied the established and strictly standardised RBA procedure for Switzerland, in which arthropods were collected during seven weeks in the period of highest arthropod abundance (Duelli and Obrist 2005; Obrist and Duelli submitted). Traps were opened between June 13th and 15th 2006 (depending on cities) and then emptied weekly until closure between August 1st and 3rd 2006. At each of the 96 locations, surface dwelling arthropods were sampled using three pitfall traps (cups), whereas flying invertebrates were sampled using so-called combination traps (Duelli et al. 1999). Subsequently, and in order to prevent stochastic influences such as bad weather or damaged traps that accidentally reduced the arthropod volume of the weekly samplings, the four weekly samples with the highest volume were chosen (see Supplementary material B for exceptions). Higher volume corresponds to more species (Smith et al. 2006a), although there might be exceptions in cases of species outbreaks or swarming events. These four weekly catches per trap location were sorted into 29 taxonomic groups which allowed expert classification of arthropod groups according to five functional groups within three categories (Table 1): trophic levels (zoophagous (including parasites), phytophagous), pollinator function and mobility (low mobility was defined as < 200m per lifetime and high as > 200m). Morphospecies were counted in each of these 29 taxonomic groups. The arthropods groups Diptera, Collembola, Acari and juvenile spiders were excluded from the analysis as their morphospecies count results in unreliable counts and exaggerated costs (Duelli and Obrist 2005; unpublished data). Seven arthropod groups were identified to the named species level (Table 1) and we used these 'true' species numbers for statistical analysis. Due to the high correlation between 'morphospecies' and ‘species’, and to simplify the text, we will use ‘species’ as a unified expression.

2.3.3 Environmental variables

We asked property owners with a questionnaire for the age of their green spaces, which we defined as the time since the last important structural modification or renewal of the green area (reflecting succession). To quantify the management variable, we counted the number of cuts of the grass or meadow plots during regular visits over the whole vegetation period (26 weeks from mid-April to mid-October). Impervious area expresses the percentage of area within a 50m radius around the trap locations (100 % = 0.79ha) that is sealed or covered by buildings. Within the same 50m radius, vegetation structures were mapped in the field and later digitized using Geographic Information Systems (ArcGIS 9.2, ESRI Redlands, USA) in order to obtain information on structural heterogeneity. We attributed structural habitat variables to four categories: 1) Hard cover area: impervious surfaces (built and sealed area), paving-stones and washed grit; 2) Monotonous ground vegetation: meadows and lawns mown > 3 times a year, ground-covering shrubs, vegetables, ornamental flowers, unwashed grit and open earth; 3) Bushes and trees < 3m; 4) Meadow: complex structured meadows (mown ≤ 3 times a year). All habitat patches sum to 100%. Trees > 3m have not been taken into account since previous studies showed that the trap types used (in top soil and 1.5 m above ground) do not representatively sample arboreal arthropods (Wermelinger et al. 2007). We calculated the heterogeneity variables based on these four habitat categories. Heterogeneity of a landscape includes two concepts: 1) Composition refers to the area fractions of the different habitat types within the area of interest (here: 50m radius), which we measured with the Shannon Index (Jonsen and Fahrig 1997; McGarigal and Marks 1995). 2) Configuration reflects the spatial distribution of individual habitat patches and includes information on the relative position to one another (McGarigal and Marks 1995). The quantity and quality of ecotones between habitat patches are suspected to strongly influence arthropod species richness. Thus, Mean Edge Contrast Index was chosen to represent configuration

(McGarigal and Marks 1995), which often explains most variation among several potential measures for edge contrast (Cushman et al. 2008). The Mean Edge Contrast Index equals the sum of the perimeter segment lengths multiplied by their corresponding contrast weights, divided by total perimeter. We assigned values to ecotones to obtain contrast weights (between 0 and 1), which reflect the following expected habitat contrasts for arthropod species richness: ecotone 'hard cover area vs. monotonous ground vegetation': contrast weight of 0.25; hard cover area vs. bush & trees: 0.5; hard cover area vs. meadow: 0.75; monotonous ground vegetation vs. bush: 0.25; monotonous ground vegetation vs. meadow: 0.5; bush vs. meadow: 0.25. The size of the grid cells chosen to calculate these indices is critical for spatial pattern detection (Wu 2004). We chose a 1 x 1m grid size to represent the appropriate scale for arthropods in urban areas, because a) most arthropods are fine-scale oriented and b) habitat types in urban context change within small distances due to varied human uses. Mean Edge Contrast Index and Shannon Index (referred to as 'heterogeneity variables') were both calculated with the software FRAGSTATS (McGarigal et al. 2002). The environmental variables and their mean values are shown in Table 2.

2.3.4 Statistical analysis

Linear mixed-effects models with a normal error distribution were used to analyse the relationship between species richness and the environmental variables. This modelling technique was chosen since the residuals were found to conform to the assumptions of homoscedasticity and normality (Crawley 2007), which is expected for count data with a mean > 30. Study locations are geographically aggregated within cities, so 'city' was treated as a random factor in the models. All explanatory variables were continuous and were tested for pair-wise correlation. All correlations remained below $r = 0.7$ which had been defined as the maximal accepted limit of correlation. Management, Mean Edge Contrast Index, and Shannon Index were expected to exhibit a curvilinear behaviour and were therefore included as linear and quadratic terms into the modelling.

For model selection, we followed an information-theoretic approach (Burnham and Anderson 2002; Johnson and Omland 2004) in which a-priori models were ranked according to their support by the data using Akaike weights obtained from the Akaike’s Information Criterion corrected for small sample size (AICc). We defined 32 candidate models (Supplementary material C), resulting from all possible combinations of the five variables (three urban and two heterogeneity variables) and the Null model (no environmental variables included, assuming random distribution). The models with AICc weights above 5% were defined as the most parsimonious set of models. We predicted total species number and species numbers of the five functional groups for each of the five environmental variables based on this set. Species numbers were allowed to vary within the limits of the focal gradient, while the remaining variables in the model were held at their respective mean values. We based each prediction on 1000 bootstrap samples of equal size to the original data set by random sampling with replacement. For each bootstrap sample, we recalculated the model parameter estimates. Finally, the predictions for each model were averaged based on their AICc weights (Burnham and Anderson 2002), estimating coefficients, and standard deviations (SD). The advantages of these new modelling and prediction techniques are that the effect size and a related error term of the gradients can be illustrated directly. In this way, the effect estimate is not based on only one single best model but on an average effect of several good models.

Based on their content of environmental predictors, the 32 possible a-priori models were attributed to one of the four model sets URBAN VARIABLES, HETEROGENEITY VARIABLES, URBAN AND HETEROGENEITY VARIABLES and NULL MODEL (Supplementary material C). Summarising single models in such model sets allows a comparison of their relative importance, i.e. urban variables versus heterogeneity variables. In addition, we calculated an estimate for Goodness-of-fit for all linear mixed effect models, which takes into account that study locations are aggregated in cities (Xu 2003). All statistical calculations were carried out with the program R v2.6.0 (R Development Core Team 2007) using library nlme (Pinheiro et al. 2008).

2.4 Results

Approximately 310’000 arthropod specimens were included in the analysis with an average of 284 (SD=45) species found per location (range 169 – 361) with little variation between cities (Fig. 1). Little variation between cities was similarly found in the five functional groups, which summed to an average of 158 zoophagous, 104 phytophagous, 47 pollinator, 178 low mobility and 85 high mobility species (Fig. 1).

2.4.1 Predictions of environmental variables

Table 3 shows the details of the a-priori models for each of the six species numbers, which we considered as the most parsimonious model set (models with AICc weights >5%). Overall, we discern two selection patterns based on AICc weights: Model numbers 11, 17 and 21 (Supplementary material C) were selected for total, phytophagous, pollinator and high mobility species numbers, whereas models 0, 1, 2 and 6 were selected to best explain zoophagous and low mobility species richness. In Fig. 2 we predict total species number and the species number of the five functional groups based on the selected models (Table 3). Increasing age and increasing configuration exhibit a noticeable and positive effect on total species number (Fig. 2A). For the age gradient, the absolute number of total species richness is predicted to increase from 274 for a one year old urban area to 310 species for an area that is 150 years old, even though SD increases rapidly for locations >90 years (Fig. 2A). For configuration, species richness is predicted to increase from 273 species for an area with limited ecotones to 337 species for the most heterogeneous area with many ecotones, but high prediction uncertainty is shown by large SD for Edge Contrast Mean Index >38 (Fig. 2A). Composition also had a positive, but less pronounced, effect with species numbers rising from 273 for an area with only few habitat types (high SD for low Shannon Diversity values) to 290 species with several habitat types. Increasing the fraction of impervious area from 3% to 92% means a reduction from 296 to 273 species, whereas increasing management intensity from zero meadow cuts to 20 lawn cuts accounts for a marginal decrease from 289 to 282 species. The negative effect of increasing management, however, levels off after approximately six cuts, and prediction insecurity increases. Poorly predicted species numbers, shown by an increasing SD, were mainly due to small sample numbers in this range of the gradient or to true high variability in species numbers. Phytophagous species richness is predicted quite precisely (Fig. 2C). Increasing age and configuration have pronounced positive effects, while habitat composition seems to reach a plateau above a Shannon Diversity Index of ca. 1.1 (min. 0.34 – max. 1.32). Pollinator species numbers (Fig. 2D) are also positively influenced by the two heterogeneity variables but these influences are less pronounced than for other groups. No influence of the three urban variables age, management intensity and impervious area on pollinators was found. Richness of highly mobile species (Fig. 2E) clearly augments with increasing age, configuration and composition, while it decreases with increasing impervious area. Management intensity does not have an effect. Zoophagous (Fig. 2B) and low mobility species richness (Fig. 2F) are explained only to a limited extent by the variables chosen. Therefore, predictions also had either high standard deviations when showing positive (age of the green area) or negative correlations (impervious area), or showed no correlation at all with the variable under examination (management, configuration and composition). The similar pattern of zoophagous and low mobility species is explained in that both groups are made up, to a large extent, of the 'remaining hymenoptera' (Table 1). Remaining Hymenoptera account for 60.0% (SD + 7.9%) of the zoophagous species richness and 53.1% (+ 7.3%) of the low mobility species richness.

2.4.2 Environmental variables according to model groups

Table 4 summarises all 32 a priori models in model sets to compare their Goodness of fit (R^2) and AICc weights. While the a-priori models explain on average a reasonable amount of the variation for total species number (R^2 = 14.1%) and phytophagous (16.7%), pollinator (17.8%) and high mobility species richness (17.1%), they explain about half as much variation for zoophagous and low mobility species numbers (R^2 of 8.4% and 7.7%, respectively). The rather poor fit of the data to the a-priori models for zoophagous and low mobility species numbers is confirmed in that selected models for these groups include the Null model (Table 3).

On average, a-priori models of the model set URBAN AND HETEROGENEITY VARIABLES consist of more variables than the remaining model sets. Models with more variables always explain more of the total variation by chance alone and thus reach higher goodness of fit values (Peres-Neto et al. 2006). In order to avoid this problem, the mean AICc weight, which is corrected for the number of parameters, is preferred to the mean R^2 to compare the different model sets. The set URBAN VARIABLES (age, impervious area, management) is most important for total species numbers (mean model weight of 4.3%). An average model of the model set HETEROGENEITY VARIABLES (configuration, composition) attains a higher mean model weight for phytophagous (7.4%), pollinator (8.9%), and high mobility species numbers (4.2%) while the URBAN VARIABLES are now negligible. For these species numbers the models of the set HETEROGENEITY VARIABLES are thus more important than the remaining models and, as models are selected based on this weight value, they affect their respective predictions more. The NULL MODELS of zoophagous and low mobility species numbers obtain high mean weight values (23.3% and 34.5%, respectively), which makes is difficult to draw conclusions as to the relative influence of the model sets (mean weight of 9% for zoophagous, 7.6% for low mobility species).

2.5 Discussion

It has been suggested that regional influences on urban arthropods are limited, while local differences in environmental variables within cities cause large effects on arthropod diversity (Niemela et al. 2002). In the present study, we investigated the influence of five such local environmental gradients on total arthropod species numbers and on species numbers within functional categories representing trophic, pollinator and mobility guilds.

The average arthropod species number in our urban study locations is 284 (range 169–361; n=96, one sampling year). These values are comparable with those of other environments outside cities when the same method was applied (Duelli and Obrist 2005; Obrist and Duelli submitted). An average forest sampling location yielded 232 species (69-473; 15 locations; 8 years) while an average agricultural area resulted in 317 species (161-470; 15 locations; 8 years). Urban areas host many arthropod species and cannot be regarded as species-poor environments.

2.5.1 Reasons for high species richness

The reasons for the high species numbers in urban areas despite habitat loss trough impervious area are multifaceted. We suspect historical and physical causes that are partially represented by our five variables. Some species survive on small grassland patches that previously formed part of large-scale meadows. The generally warmer climate in cities has allowed the survival and/or immigration of arthropod fauna from seminatural dry-meadows (Germann et al. 2008), which is a habitat type that has become rare in Central European agricultural landscapes. In addition, and again due to the urban heat island effect, a considerable number of Mediterranean species have invaded cities and exotic species are able to survive (or even thrive) in urban habitats after accidental introduction by man (Germann et al. 2008; Kouakou et al. 2008). Urban areas have been identified as the points of origin for invasive arthropods (Matteson et al. 2008; Ward and Harris 2005). The urban mosaic is characterised by the fact that many different habitat types are spatially close. Furthermore, ecotones created by boundaries usually offer additional resources and micro-conditions that are absent in the habitat types. The spatial proximity, the habitat mix and the ecotones probably offer diverse ecological niches and resources which meet the different needs at different life cycle stages of many species (egg and larval development, reproduction). In this way, the co-existence of many species is enabled.

The spatial proximity of different habitat types in the urban mosaic might to be responsible for another effect observed in our study: in their quest for good habitats arthropods often cross the boundaries of their native fine-scale habitat plots. In doing so, they are expected to arrive regularly in suboptimal habitats. This process may explain why species numbers in 'good' and 'bad' study locations (i.e., old and heterogenous vs young and monotonous plots) did not differ as much as expected, since isolation and fragmentation through impervious areas may not represent a major difficulty for moving arthropods (Angold et al. 2006). Species occurring in cities are suspected to have been selected to overcome such obstacles.

2.5.2 Urban variables

We suspect that the positive correlation between total species richness and age of the green area is based on the combined effects of species accumulation through stochastic local immigration over time and species-specific occupation of ecological niches that increase with the plots succession. Despite the fact that succession is not always correlated with vegetation growth, and will never reach a sort of climax state due to persisting human impact (cutting trees, bushes, meadows), the number of ecological niches is generally expected to increase with age (Rebele 1994).

Increasing management had a minor negative influence on total species richness. We expected to observe a higher negative influence of increased management as found by previous studies on roundabouts (Helden and Leather 2004). We attribute this finding to methodological issues which are inherent to the mosaic structure of urban areas. In our study, management, i.e. the number of cuts, was measured within a radius of 5m around the traps. Grass or meadow plot sizes, however, range from 20 m^2 to 10000 m^2. These varying plot sizes add an unknown component to our measurement of management intensity. Small intensively managed plots are likely to be invaded from surrounding, less intensively managed areas and in this way a negative effect of intensive management might be masked. This hypothesis is supported by the results on heterogeneity (see below).

Sealed and built areas are generally regarded as hostile habitats that prevent high biodiversity because there is limited vegetation cover and low plant diversity. Smith et al. (2006b) documented the expected negative effect of impervious area on total arthropod richness. Even more pronounced are the negative effects of urbanisation in broad-scale rural-urban gradients (McDonnell and Hahs 2008). At our finer scale (0.79 ha) and within cities, we also found a negative influence of impervious area on total species richness from 296 to 273 species only (7.8%) on the observed gradient (from 3% to 92% impervious area). Possibly a sealed radius of 50m does not represent a major barrier for flying insects. For zoophagous species the measured effect was clearly negative, corroborating findings of Denys and Schmidt (1998) who had found a pronounced negative urbanisation effect on parasitoid species. Phytophagous species in our study, however, experience a less pronounced negative effect than both polyphagous and monophagous species of their study.

2.5.3 Heterogeneity variables

The two indices for structural heterogeneity (Edge Contrast Mean Index for configuration and Shannon Index for composition) represent indicators for the urban mosaic. In urban areas past and present human activity has replaced large-scale environmental gradients with many different fine-scale habitat types (e.g. meadow, bushes, ornamental plants, vegetable gardens, lawns, buildings etc.) which we measured with the Shannon composition index. The urban habitat matrix is characterised by both diffuse and abrupt transition zones (ecotones) which we measured with the Edge Contrast Mean Index for configuration. We found that urban arthropod species richness is positively linked to both heterogeneity measures (composition and configuration) which is similar to the findings of previous studies on arthropods outside urban habitats (Duelli 1997; Jonsen and Fahrig 1997; Niemela et al. 1996). The heterogeneity effect is very pronounced for phytophagous and pollinator species. Although not measured directly, we can safely assume that increased heterogeneity implicitly brings increased plant species richness (Kumar et al. 2006). As 88.4 % of the pollinator species are also phytophagous (Table 1), and a relevant fraction of phytophagous species are host plant specific (Smith et al. 2006b), we suspect that plant species richness is the causal link for the positive correlation between functional groups and heterogeneity, as has been shown in previous studies (Haddad et al. 2001; Siemann et al. 1998). Overall, the sheer diversity and quantity of ecotones in the urban area seem to be very important for urban arthropods.

Grouping the statistical models into model sets (URBAN VARIABLES, HETEROGENEITY VARIABLES, URBAN AND HETEROGENEITY VARIABLES) allows the identification of important variable sets. Considering the mean weight, the heterogeneity variables (configuration, composition) are most important for phytophagous, pollinator and high mobility species numbers (Table 4), whereas the urban variables (age, impervious area, management) are most important for zoophagous and low mobility species numbers. However, looking at the mean Goodness-of-fit (R2 in Tables 3, 4), the variance in low mobile and zoophagous species is explained rather poorly by our variables. This result is similar to the findings of Smith et al. (2006b) who also found that species numbers of less mobile groups were poorly explained by fine-scale variables. These counter-intuitive results are difficult to explain but we suspect that the urban mosaic characteristics are one of the reasons. Good and bad habitats are close to each other and there is a continuous flux of species in and out of these small patches, even in species with low mobility (Angold et al. 2006). The similar response of the two functional groups is partially explained by the fact that the ‘remaining Hymenoptera’ represent >50% of the species numbers for both groups.

2.5.4 Conclusions

Local species richness of arthropods, as well as the related functional diversity of trophic, pollinator and mobility guilds, do not appear to be vitally threatened by the extent of urbanisation within the three investigated Swiss cities. Total species numbers and species richness of the functional groups are comfortingly high when compared to values of other semi-natural areas. At least some urban habitats seem to support many species.

Urban areas offer unique opportunities that are exploited by arthropods. The generally warmer climate in cities allows the survival of thermophile arthropods which do not live in surrounding landscapes. The close-knit urban mosaic offers many ecological niches that are often exclusive for cities. These factors, represented by two heterogeneity indices in our study, are expected to facilitate the co-existence of many species in cities (Rebele 1994). Other urban characteristics such as repeated human influence through planning decisions and human management (represented by the urban variables age, impervious area, management) influence species richness both in the long and the short term.

On the one hand, high arthropod richness is a pre-requisite for resilience and ecosystem services. The quantification of the influence of varying levels of species richness on resilience, knowledge on functional links among species is essential – a point which was not investigated in this study. On the other hand such a high biodiversity offers a wealth of experience for city dwellers. In the face of current and future densification of urban areas, we propose counteractions to maintain or even improve species richness in urban areas. We recommend planning the remaining urban green as heterogeneous habitats, and managing it as extensively as the local human exigencies allow. Urban areas are built for humans and thus actions in favour of biodiversity will only persist if they consider the use and perceptions of their human inhabitants. Studies on human preferences of landscapes show that city inhabitants prefer heterogeneous landscapes (Home et al. submitted) indicating that arthropod and human requirements for good urban habitats are aligned. These are important messages for city planners and managers willing to positively influence urban biodiversity.

Acknowledgements

We thank the house owners that provided access to their properties and the authorities of Lucerne, Lugano and Zurich for their support of the project. We are grateful to V. Albin, J. Ambrosini, J. Bolliger, F. Bontadina, T. Fabbro, B. Fecker, F. Fibbioli, S. Fontana, F. Gebreselassie, D. Häring, R. Home, W. Kastenholz, F. Kienast, M. Kindermann, L. Milani, A. Niederer, J. Pellet, M. Ryf, M. Schaub, A. Schulz, R. Siegwart, R. Tester and P. Wirz who helped in the field, in the lab, with statistical questions or the organization of the project. The following arthropod specialists supported us by determining the species: C. Canepari (Coccinelidae), Y. Chittaro (Carabidae), P. Duelli (Neuroptera), C. Germann (Curculionidae), X. Heer (Araneae), C. Pradella (Lucanidae, Buprestidae, Cerambycidae). F. Bontadina, R. Home and M. Schaub improved earlier versions of the manuscript. Special thanks go to M. Lehmann.

This study forms part of the interdisciplinary project 'BiodiverCity' (www.biodivercity.ch) which aims at the identification, maintenance and enhancement of biodiversity and their acceptance in the urban development process. BiodiverCity was funded by the Swiss National Science Foundation as a project of NRP54 'Sustainable development of the built environment' (www.nrp54.ch).

2.6 References

Angold P.G., Sadler J.P., Hill M.O., Pullin A., Rushton S., Austin K., Small E., Wood B., Wadsworth R., Sanderson R. and Thompson K. 2006. Biodiversity in urban habitat patches. Science of the Total Environment 360: 196-204.

Bengtsson J., Engelhardt K., Giller P., Hobbie S., Lawrence D., Levine J., Villa M. and Wolters V. 2002. Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. In Loreau M., Naeem S. and Inchausti P. (eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.

Bundesamt für Statistik 2005. Arealstatistik Schweiz: Zahlen – Fakten – Analysen, Neuchâtel p. 99.

Burnham K.P. and Anderson D.R. 2002. Model Selection and Multimodel Inference: a practical information-theoretic approach. Springer-Verlag, New York.

Crawley M.J. 2007. The R Book. John Wiley & Sons Ltd, Chichester.

Cushman S.A., McGariyal K. and Neel M.C. 2008. Parsimony in landscape metrics: Strength, universality, and consistency. Ecological Indicators 8: 691-703.

de Vries S., Verheij R.A., Groenewegen P.P. and Spreeuwenberg P. 2003. Natural environments – healthy environments? An exploratory analysis of the relationship between greenspace and health. Environment and Planning A 35: 1717-1731.

Denys C. and Schmidt H. 1998. Insect communities on experimental mugwort (Artemisia vulgaris L.) plots along an urban gradient. Oecologia 113: 269-277.

Duelli P. 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agriculture Ecosystems & Environment 62: 81-91.

Duelli P. and Obrist M.K. 2003. Biodiversity indicators: the choice of values and measures. Agriculture Ecosystems & Environment 98: 87-98.

Duelli P. and Obrist M.K. 2005. Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). Schriftenreihe der Forschungsanstalt Reckenholz 56: 132-138.

Duelli P., Obrist M.K. and Schmatz D.R. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture Ecosystems & Environment 74: 33-64.

Dunn R.R., Gavin M.C., Sanchez M.C. and Solomon J.N. 2006. The pigeon paradox: Dependence of global conservation on urban nature. Conservation Biology 20: 1814-1816.

Elliot R. 1992. Intrinsic Value, Environmental Obligation and Naturalness. The Monist 75: 138-60.

Fuller R.A., Irvine K.N., Devine-Wright P., Warren P.H. and Gaston K.J. 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3: 390-394.

Fuller R.M., Smith G.M., Sanderson J.M., Hill R.A., Thomson A.G., Cox R., Brown N.J., Clarke R.T., Rothery P. and Gerard F.F. 2002. Countryside Survey 2000 Module 7. Land Cover Map 2000. Final Report CSLCM. Centre for Ecology and Hydrology, Monks Wood, UK.

Germann C., Sattler T., Obrist M.K. and Moretti M. 2008. Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 81 141-154.

Grimm N.B., Faeth S.H., Golubiewski N.E., Redman C.L., Wu J.G., Bai X.M. and Briggs J.M. 2008. Global change and the ecology of cities. Science 319: 756-760.

Haddad N.M., Tilman D., Haarstad J., Ritchie M. and Knops J.M.H. 2001. Contrasting effects of plant richness and composition on insect communities: A field experiment. American Naturalist 158: 17-35.

Helden A.J. and Leather S.R. 2004. Biodiversity on urban roundabouts – Hemiptera, management and the species-area relationship. Basic and Applied Ecology 5: 367-377.

Home R., Bauer N. and Hunziker M. submitted. Estimating the effect of visual elements and information on landscape preference.

Hunter L. and Rinner L. 2004. The association between environmental perspective and knowledge and concern with species diversity. Society and Natural Resources 17: 517- 532.

Johnson J.B. and Omland K.S. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19: 101–108.

Jonsen I.D. and Fahrig L. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12: 185-197.

Kouakou D., Sattler T., M.K O., Duelli P. and Moretti M. 2008. Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 81 191-198.

Kumar S., Stohlgren T.J. and Chong G.W. 2006. Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87: 3186-3199.

Legendre P. and Legendre L. 1998. Numerical ecology. Elsevier Science PV, Amsterdam.

Loreau M., Downing A., Emmerson M., Gonzalez A., Hughes J., Inchausti P., Joshi J., Norberg J. and Sala O. 2002. A new look at the relationship between diversity and stability. In

Loreau M., Naeem S. and Inchausti P. (eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives, pp. 79–91. Oxford University Press, Oxford.

Loreau M., Mouquet N. and Gonzalez A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences of the United States of America 100: 12765-12770.

Matteson K.C., Ascher J.S. and Langellotto G.A. 2008. Bee richness and abundance in New York city urban gardens. Annals of the Entomological Society of America 101: 140-150.

McDonnell M.J. and Hahs A.K. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23: 1143-1155.

McGarigal K., Cushman S.A., Neel M.C. and Ene E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst.

McGarigal K. and Marks B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service. Pacific North West Research Station 351, Portland, OR. p. 141.

McIntyre N.E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America 93: 825-835.

McIntyre N.E., Rango J., Fagan W.F. and Faeth S.H. 2001. Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52: 257-274.

Miller J.R. 2005. Biodiversity conservation and the extinction of experience. Trends in Ecology & Evolution 20: 430-434.

Moretti M., Duelli P. and Obrist M.K. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149: 312-327.

Niemela J., Haila Y. and Punttila P. 1996. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19: 352-368.

Niemela J., Kotze D.J., Venn S., Penev L., Stoyanov I., Spence J., Hartley D. and de Oca E.M. 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology 17: 387-401.

Obrist M.K. and Duelli P. 1996. Trapping efficiency of funnel- and cup-traps for epigeal arthropods. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 69: 367-369.

Obrist M.K. and Duelli P. submitted. Rapid Biodiversity Assessment (RBA) of arthropods for monitoring average local species richness and related ecosystem services. Biodiversity and Conservation.

Oliver I. and Beattie A.J. 1993. A Possible Method for the Rapid Assessment of Biodiversity. Conservation Biology 7: 562-568.

Peres-Neto P.R., Legendre P., Dray S. and Borcard D. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87: 2614-2625.

Pinheiro J., Bates D., DebRoy S., Sarkar D. and R Core team. 2008. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-89.

R Development Core Team 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rapport D.J., Costanza R. and McMichael A.J. 1998. Assessing ecosystem health. Trends in Ecology & Evolution 13: 397-402.

Rebele F. 1994. Urban Ecology and Special Features of Urban Ecosystems. Global Ecology and Biogeography Letters 4: 173-187.

Sanford M.P., Manley P.N. and Murphy D.D. 2009. Effects of Urban Development on Ant Communities: Implications for Ecosystem Services and Management. Conservation Biology 23: 131-141.

Siemann E., Tilman D., Haarstad J. and Ritchie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. American Naturalist 152: 738-750.

Smith R.M., Gaston K.J., Warren P.H. and Thompson K. 2006a. Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. Biodiversity and Conservation 15: 2515-2545.

Smith R.M., Warren P.H., Thompson K. and Gaston K.J. 2006b. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15: 2415-2438.

Tzoulas K., Korpela K., Venn S., Yli-Pelkonen V., Kazmierczak A., Niemela J. and James P. 2007. Promoting ecosystem and human health in urban areas using Green Infrastructure: A literature review. Landscape and Urban Planning 81: 167-178.

United Nations 2008. World Urbanization Prospects: the 2007 Revision. United Nations, New York.

Walker, B., Holling, C. S., Carpenter, S. R. and Kinzig, A. 2004. Resilience, adaptability and transformability in social ecological systems. Ecology and Society 9: 5 [online].

Ward D.F. and Harris R.J. 2005. Invasibility of native habitats by Argentine ants, Linepithema humile, in New Zealand. New Zealand Journal of Ecology 29: 215-219.

Wermelinger B., Flückiger P.F., Obrist M.K. and Duelli P. 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. Journal of Applied Entomology 131: 104-114.

Whittaker R.J., J. W.K. and Field R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28: 453-470.

Wu J.G. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19: 125-138.

Xu R.H. 2003. Measuring explained variation in linear mixed effects models. Statistics in Medicine 22: 3527-3541.

2.7 Tables and figures

Table 1: Twenty-nine taxonomic arthropod groups, mean species number per study location and attribution to trophic level, pollinator function, mobility and the determination information available.

Taxa	**Mean species no**	**Trophic level**	**Pollinator function**	**Mobility**	**Species information for statistical analysis**
Arthropoda: miscellaneous					
Araneae	12.6	zoophagous		Low	Species
Remaining Arthropoda[1, 2]	7.1	No attribution		No attribution	Morphospecies
Coleoptera					
Carabidae[1]	4.4	zoophagous		Low	Species
Staphylinidae	13.1	zoophagous		Low	Morphospecies
Silphidae	0.2	zoophagous		Low	Morphospecies
Oedemeridae	2.8	phytophagous	Pollinator	High	Morphospecies
Scarabeidae	1.9	phytophagous	Pollinator	High	Morphospecies
Chrysomelidae	3.6	phytophagous	Pollinator	High	Morphospecies
Curculionidae	6.9	phytophagous	Pollinator	Low	Species
Cerambycidae[1]	0.8	phytophagous	Pollinator	Low	Species
Buprestidae[1]	0.7	phytophagous	Pollinator	High	Species
Coccinellidae	2.8	zoophagous	Pollinator	High	Species
Cantharidae	0.6	zoophagous	Pollinator	High	Morphospecies
Cleridae	0.9	zoophagous	Pollinator	High	Morphospecies
Elateridae	1.5	phytophagous		High	Morphospecies
Scolytinae	0.9	phytophagous		High	Morphospecies
Remaining Coleoptera[1]	13.8	No attribution		No attribution	Morphospecies
Hymenoptera					
Formicidae worker	4.9	zoophagous		Low	Morphospecies

Vespidae & Formicidae (winged)	15.7	zoophagous		High	Morphospecies
Apoidea	17.9	phytophagous	Pollinator	High	Morphospecies
Symphyta	1.2	No attribution	Pollinator	High	Morphospecies
Remaining Hymenoptera	94.4	zoophagous		Low	Morphospecies
Hemiptera					
Zoophagous Heteroptera[3]	3.9	zoophagous		Low	Morphospecies
Remaining Heteroptera	17.1	phytophagous		Low	Morphospecies
Homoptera[1]	25.9	phytophagous		High	Morphospecies
Insecta: miscellaneous					
Neuropterida[1]	1.9	zoophagous		High	Species
Psocoptera[1]	3.6	phytophagous		Low	Morphospecies
Thysanoptera[1]	13.8	phytophagous		Low	Morphospecies
Lepidoptera[1]	7.4	phytophagous	Pollinator	High	Morphospecies

[1] represents the taxonomic groups of the original RBA (Duelli and Obrist 2005) whereas the remaining taxa are subgroups of former higher level groups

[2] Chilopoda, Diplopoda, Isopoda, Orthoptera, Ephemeroptera, Plecoptera, Odonata

[3] Reduviidae, Nabidae, Phymatidae, Anthocoridae, Saldidae, Hydrocorisae

Table 2: Mean and range (minimum and maximum) of the five environmental variables for each city separately and for the three cities summarised.

	Lugano		Lucerne		Zurich		3 cities	
Variable	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
Management intensity [1]	7	1 – 20	6	0 – 16	5	1 – 13	6	0 – 20
Age of green area [2]	45	1 – 106	37	1 – 156	41	1 – 156	41	1 – 156
Impervious area [3]	48.7	10.6 – 85.2	48.3	6.5 – 86.3	50.2	2.5 – 91.8	49.1	2.5 – 91.8
Configuration [4]	32.5	25.2 – 47.5	30.8	24.3 – 39.1	32.0	23.8 – 42.6	31.8	23.8 – 47.5
Composition [5]	1.02	0.47 – 1.32	1.03	0.49 – 1.31	0.96	0.34 – 1.29	1.01	0.34 – 1.32

[1] number of cuts

[2] years

[3] % in 50m radius

[4] FRAGSTATS Mean Edge Contrast Index

[5] FRAGSTATS Shannon-Index

Table 3: Selected linear mixed-effects models for species numbers of total arthropod species and five functional groups (out of 32 models). Environmental variables included in models are shown with X. Per explained species number, models are ranked according to AICc weights. k is the number of parameters in the model. The minimum of three parameters for the Null model (no. 0 assuming ran-dom distribution of species numbers) comprises intercept, random factor city and unexplained variance.

	Model No.	**Age of green area**	**Impervious area**	**Management intensity**	**Configuration**	**Composition**	**k**	**Delta AIC$_c$**	**AIC$_c$ Weight**	**R^2**
Total species number	21	X			X	X	8	0.00	17.0%	22.3%
	17	X	X		X		7	0.16	15.7%	18.5%
	11		X		X		6	1.65	7.5%	13.4%
	7	X		X			6	1.99	6.3%	13.1%
	1	X					4	2.16	5.8%	4.9%
	3			X			5	2.31	5.3%	8.8%
Zoophagous	1	X					4	0.00	23.8%	4.3%
	0						3	0.04	23.3%	0.0%
	2		X				4	0.79	16.0%	3.5%
	6	X	X				5	0.90	15.2%	7.6%
Phytophagous	21	X			X	X	8	0.00	51.1%	29.1%
	15				X	X	7	2.02	18.6%	24.3%
	11		X		X		6	4.20	6.3%	18.4%
	28	X	X		X	X	9	4.25	6.1%	29.3%
	17	X	X		X		7	4.63	5.1%	21.5%
Pollinator	21	X			X	X	8	0.00	26.3%	27.7%
	15				X	X	7	0.45	21.0%	24.0%
	11		X		X		6	1.57	12.0%	18.8%
	5					X	5	3.11	5.6%	14.7%
	14			X		X	7	3.14	5.5%	22.0%

High mobility	21	X			X	X	8	0.00	52.1%	28.6%
	17	X	X		X		7	2.85	12.5%	22.6%
	15				X	X	7	3.17	10.7%	22.8%
	11		X		X		6	3.82	7.7%	18.3%
	28	X	X		X	X	9	4.39	5.8%	28.6%
Low mobility	0						3	0.00	34.5%	0.0%
	1	X					4	1.05	20.5%	3.2%
	2		X				4	1.66	15.0%	2.6%
	6	X	X				5	2.86	8.3%	5.6%

Table 4: Mean AICc weight and mean R2 (Xu 2003) of all 32 a-priori models (Supplementary material C) within the four model groups (URBAN VARIABLES = 7 models, HETEROGENEITY VARIABLES = 3, URBAN AND HETEROGENEITY VARIABLES = 21 and NULL MODEL = 1) explaining the species numbers of the six functional groups. Mean AICc weight x n models add to 100%; R2 indicates the fraction of explained variation on total variation (for the Null model this is – per definition – 0%).

	Total species number		**Zoophagous**		**Phytophagous**		**Pollinator**		**High mobility**		**Low mobility**	
Model group (numbers of models in group)	Mean Weight	Mean R^2	Mean Weight	Mean R^2	Mean Weight	Mean R^2	Mean Weight	Mean R^2	Mean Weight	Mean R^2	Mean Weight	Mean R^2
URBAN VARIABLES (n = 7)	4.3%	9.3%	9.0%	6.6%	0.1%	8.0%	0.8%	10.1%	0.3%	9.1%	7.6%	5.7%
HETEROGENEITY VARIABLES (n = 3)	2.2%	9.7%	1.2%	4.2%	7.4%	15.0%	8.9%	15.1%	4.2%	14.7%	1.5%	4.2%
URBAN AND HETEROGENEITY VARIABLES (n = 21)	2.8%	17.0%	0.5%	10.0%	3.6%	20.6%	3.2%	21.6%	4.1%	20.9%	0.4%	9.2%
NULL MODEL (n = 1)	4.2%	0.0%	23.3%	0.0%	0.2%	0.0%	0.3%	0.0%	0.3%	0.0%	34.5%	0.0%
Mean of all models (n = 32)	3.1%	14.1%	3.1%	8.4%	3.1%	16.7%	3.1%	17.8%	3.1%	17.1%	3.1%	7.7%

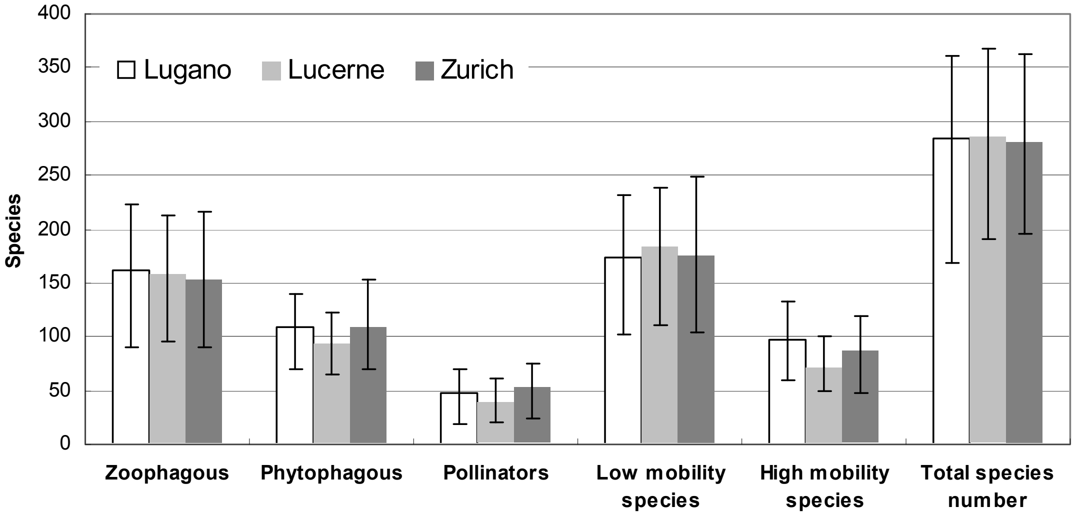

Fig. 1: Mean number and range (minimum/maximum) of total arthropod species and five functional groups in the three Swiss cities of Lugano, Lucerne and Zurich.

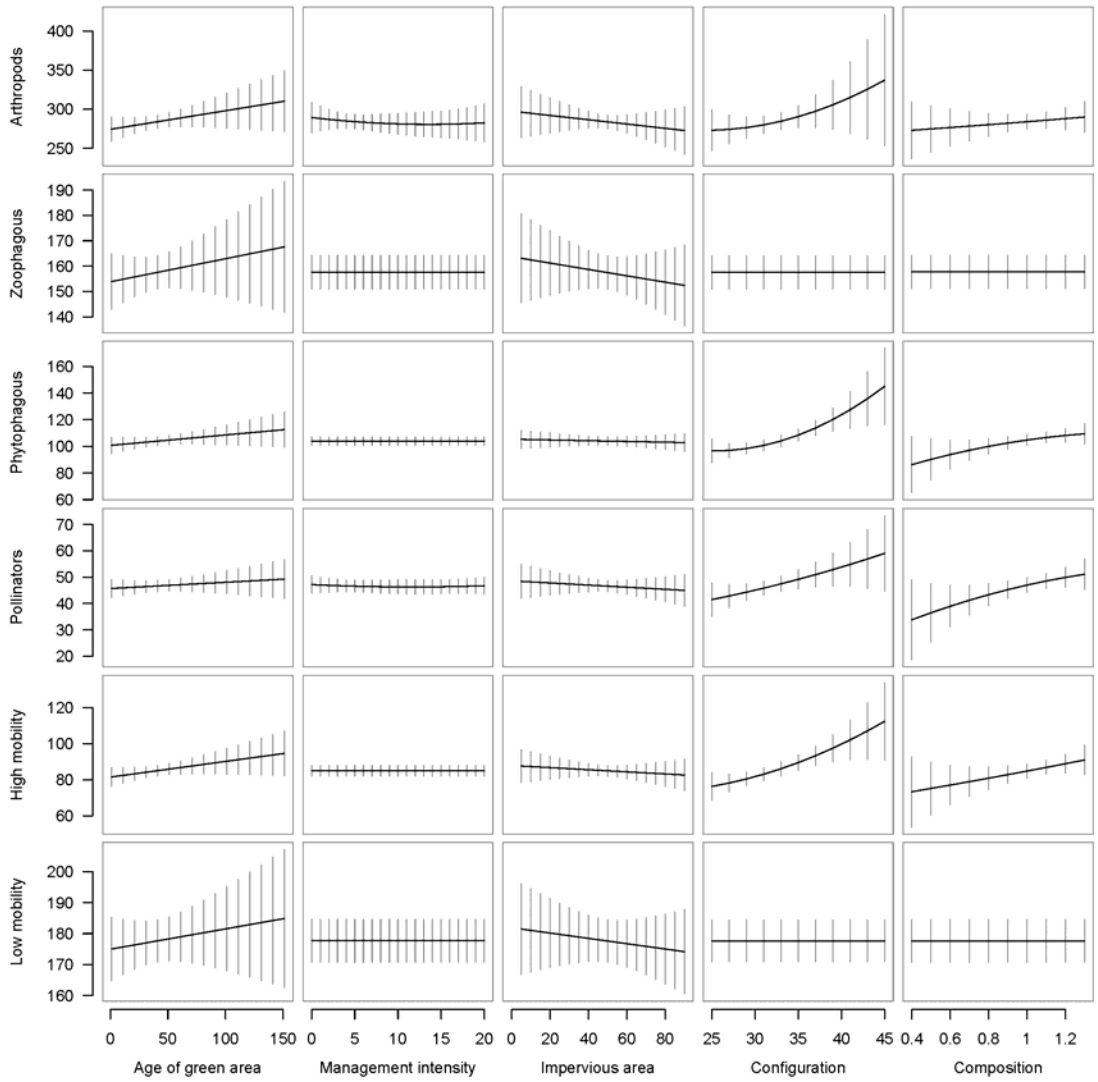

Fig. 2: Model averaged predictions (mean ± SD) for total species richness and the five functional groups across the five environmental gradients within their respective minimum and maximum. Predictions resulted by averaging selected models (Table 3) based on their AICc weights (for more information see methods). For methodological reasons (single taxonomic groups can count in several functional groups; Table 1), direct comparison of predictions is only allowed for total species number and within functional categories (delimited by black lines) which are trophic (zoophagous & phytophagous), pollinator (pollinators) and mobility (high mobility & low mobility) guilds.

2.8 Supplementary material

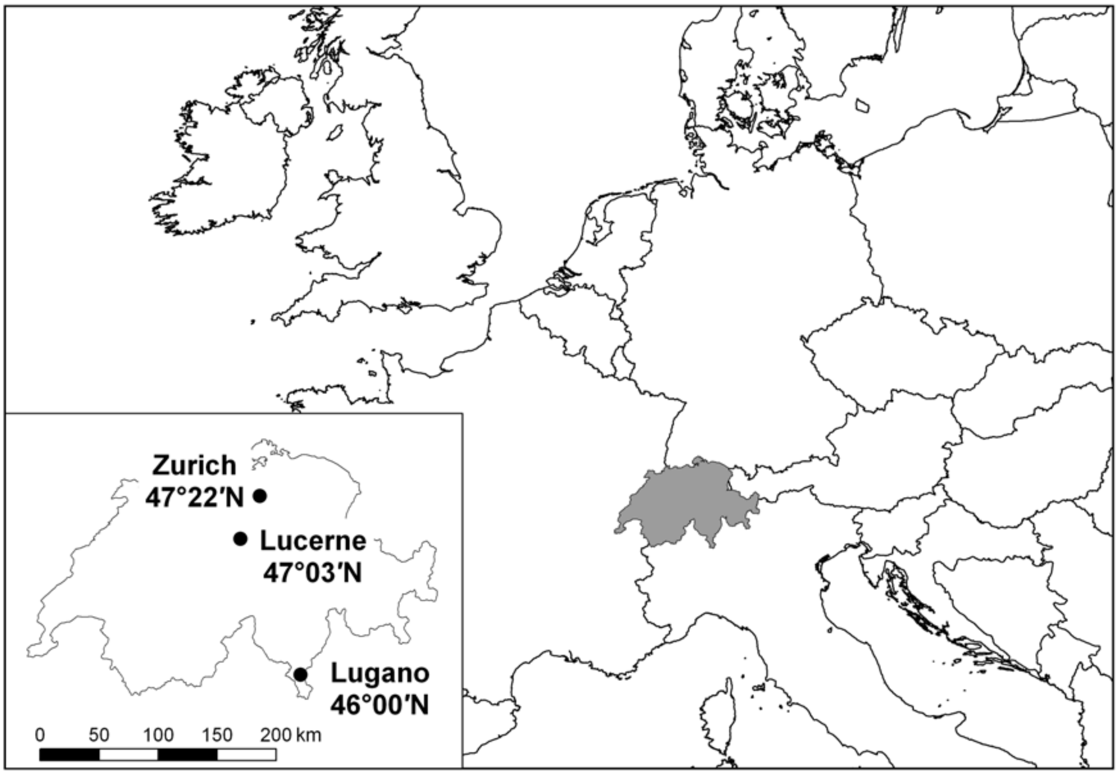

Fig. S1: Location of the three study sites, the cities of Zurich Lucerne and Lugano in Switzerland.

S2: Information on method Rapid Biodiversity Assessment (RBA)

In previous publications the method Rapid Biodiversity Assessment (RBA), as applied in Switzerland, is explained in great detail (Duelli and Obrist 2005; Obrist and Duelli submitted). Here we summarise the most important information. RBA samples arthropods during seven weeks in the period of highest arthropod abundance and subsequently selects the four weeks with largest volume for the count of morphospecies.

Every study location is established with two trap types. Surface dwelling arthropods were sampled using pitfall traps, whereas flying invertebrates were sampled using so called combination traps (Duelli et al. 1999). Pitfall traps consisted of three plastic cups recessed into the soil (opening diameter 75 mm; arranged in an isosceles triangle with a distance of one meter). Transparent roofs installed approximately 8 cm above the cups provided protection from the rain. This contrasts the original method, where only one funnel trap (150 mm diameter x 400mm depth) had been used, the cause being restrictions by property owners. But as shown by (Obrist and Duelli 1996) these two methods are near equal with respect to their trapping efficiency. The interception traps combine a non-directional window trap and a yellow water pan (diameter of 0.44 m) placed at a height of 1.5 m above ground. At each of the 96 locations, three cup traps and one combination trap were installed on a meadow or lawn plot (homogeneous within at least a radius of 5 m). Both, pitfall and combination traps, were filled with 0.2% Metatin (bactericide) solution. For both trap types, the probability of s species being caught is a function of their abundance and their activity (Duelli et al. 1999).

Duelli et al. (1999) identified the optimal time period for assessing terrestrial arthropod species richness, which still allows a reliable assessment of species numbers despite of reduced effort. The selection of seven sampling weeks with the highest species richness from mid-June to beginning of August corresponds to the warmest period in the Swiss summer. Thus, traps of the present study were opened between June 13th and 15th (depending on cities) and then emptied weekly during seven weeks until closure between August 1st and 3rd 2006. Insects were stored per location and trap type in vials containing 70 % alcohol. After the seven sampling weeks and to prevent stochastic influences like bad weather, loss or damage of traps, which accidentally reduced the arthropod volume of the weekly samplings, four weekly samples per trap type were selected: In the beginning, the first vial (mid-June) and the last vial (early August) of both trap types were selected to cover as much as possible the seasonal spectrum of the changing species composition. If, however, the volume (measured with a measuring jug in ml, without alcohol) was less than two thirds of the second or the second-last weeks, respectively, the latter were chosen instead. Of the remaining five weekly samples, the two with the highest volume were chosen, independently for the two trap types. Higher volume corresponds to more species (Smith et al. 2006), although there might be exceptions to that in cases of species outbreaks or swarming events. Only the material from the selected four weeks was processed further. This selection procedure guarantees a high correlation of the samples with the species richness of the whole year (R2= 0.92; Obrist and Duelli submitted).These four weekly catches per trap location were sorted in 29 taxonomic groups (Table 1). This was a further refinement of the original RBA method (Duelli and Obrist 2005) which attributed arthropods into 14 taxonomic groups. The refinement allowed improved expert classification of arthropod groups according to five functional groups in three categories: trophic levels (zoophagous (including parasites), phytophagous species), pollinator function and mobility (low means < 200m per lifetime, high means > 200m; Table 1). If a taxonomic group was ecologically heterogeneous with respect to the five functional groups, the group was not attributed (i.e. remaining Coleoptera, remaining Arthropoda). Morphospecies were counted in each of these 29 taxonomic groups. Two specimens were assigned to different morphospecies, if an entomologically trained but non-specialist processor could distinguish external morphological differences. With such a definition, many species with sexual dimorphism or juvenile stages could split into multiple morphospecies, whereas cryptic species were lumped into one morphospecies. Despite these constraints, species numbers obtained in this way showed for most taxa high correlation with ‘true’ species numbers (Obrist and Duelli submitted). Seven arthropod groups were identified to named species (Table 1). We used these ‘true’ species numbers for statistical analysis. The sorting of Diptera, Collembola, Acari and juvenile spiders to morphospecies resulted in unreliable counts and exagerated costs (Duelli and Obrist 2005); unpublished data), while accounting for an average volume of only 5.1 % (1.5%-10.6%) of a study locations catch. Therefore these groups were omitted from this study. Due to their high correlation of ‘morphospecies’ and ‘species’, and to simplify the text, we will use ‘species’ as a unified expression.

Table S3: Overview on all 32 linear mixed-effects models formulated a-priori which were evaluated for all six explained arthropod richness counts (total species richness, zoophagous, phytophagous, pollinator, high mobility, low mobility). Model set indicates whether the respective models consist of urban variables or of heterogeneity variables only or of combination of both variable types. Selected models are shown in Table 3. Abbreviations: age = Age of green area; impervious = Impervious area; cut+cut2 (linear and quadratic function) = Management; ECON+ECON2= Configuration (heterogeneity); SHDI+SHDI2 = Composition (heterogeneity). See methods for definition of explaining variables. Variables are aggregated within random factor 'city' (explicit formulation not shown).

Model set	Model-No.	Candidate Models
Urban variables	1	age
	2	impervious
	3	cut+cut2
	6	age+impervious
	7	age+cut+cut2
	10	impervious+cut+cut2
	16	age+impervious+cut+cut2
Heterogeneity variables	4	ECON+ECON2
	5	SHDI+SHDI2
	15	ECON+ECON2+SHDI+SHDI2
Urban and heterogeneity variables	8	age+ECON+ECON2
	9	age+SHDI+SHDI2
	11	impervious+ECON+ECON2
	12	impervious+SHDI+SHDI2
	13	cut+cut2+ECON+ECON2
	14	cut+cut2+SHDI+SHDI2
	17	age+impervious+ECON+ECON2
	18	age+impervious+SHDI+SHDI2
	19	age+cut+cut2+ECON+ECON2
	20	age+cut+cut2+SHDI+SHDI2
	21	age+ECON+ECON2+SHDI+SHDI2
	22	impervious+cut+cut2+ECON+ECON2
	23	impervious+cut+cut2+SHDI+SHDI2

	24	impervious+ECON+ECON2+SHDI+SHDI2
	25	cut+cut2+ECON+ECON2+SHDI+SHDI2
	26	age+impervious+cut+cut2+ECON+ECON2
	27	age+impervious+cut+cut2+SHDI+SHDI2
	28	age+impervious+ECON+ECON2+SHDI+SHDI2
	29	age+cut+cut2+ECON+ECON2+SHDI+SHDI2
	30	impervious+cut+cut2+ECON+ECON2+SHDI+SHDI2
	31	age+impervious+cut+cut2+ECON+ECON2+SHDI+SHDI2
Null model	0	

References cited in supplementary material

Duelli P. and Obrist M.K. 2005. Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). Schriftenreihe der Forschungsanstalt Reckenholz 56: 132-138.

Duelli P., Obrist M.K. and Schmatz D.R. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture Ecosystems & Environment 74: 33-64.

Obrist M.K. and Duelli P. 1996. Trapping efficiency of funnel- and cup-traps for epigeal arthropods. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 69: 367-369.

Obrist M.K. and Duelli P. submitted. Rapid Biodiversity Assessment (RBA) of arthropods for monitoring average local species richness and related ecosystem services. Biodiversity and Conservation.

Smith R.M., Gaston K.J., Warren P.H. and Thompson K. 2006. Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. Biodiversity and Conservation 15: 2515-2545.

3

How to manage the urban green to enhance bird species richness and diversity

How to manage the urban green to enhance bird species richness and diversity

S. Fontana[1, 2], T. Sattler[1, 3], F. Bontadina[3, 4], M. Moretti[1]

[1] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[2] Departement of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

[3] Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[4] SWILD – Urban Ecology and Wildlife Research, Wuhrstrasse 12, CH-8003 Zurich, Switzerland

Submitted to *Biological Conservation*

3.1 Abstract

Urbanization is a worldwide and rapidly increasing, high-impact environmental change. Even though urban areas are often regarded as species-poor environments, biodiversity is often surprisingly rich and can be enhanced with specific measures. Quantitative information on the effect of management measures on biodiversity is an indispensable basis for decisions by urban planners and managers, yet such information is often lacking. We observed 63 bird species and analysed the species richness and avian diversity with reference to several urban environmental gradients at 96 sampling points in three Swiss cities. With an information theoretic approach, the best models were selected out of a set of candidate models and predictions were calculated based on AICc-weights. Bird species richness and diversity are negatively affected by increasing proportions of sealed area or buildings, while increasing vegetation structures show positive effects. Trees are the major vertical green structure in the urban matrix and our models predict an increase from 13 bird species in the absence of trees to 20 species with 46% of tree cover. Tree composition analysis shows that coniferous trees help to maximize bird species richness with the models predicting 14 bird species at sites with only deciduous woody plants and an increase to 20 species at places where coniferous and deciduous plants occur at a 1:1 ratio. Increasing tree coverage reduces dominance of single species, which enhances bird species diversity. These results demonstrate clear quantitative management options that could improve avian biodiversity in urban areas.

Keywords

Urban ecology, Swiss cities, urbanization, deciduous and coniferous woody plants, urban green, structural vegetation diversity, avian biodiversity, management

3.2 Introduction

Nowadays, the majority of the human population of the world lives in cities. The proportion of these urban inhabitants is constantly growing on all continents and is expected to reach 70% by 2050 (United Nations 2008). Furthermore, the urban environment has recently gained broad attention by an increasing number of ecologists (Grimm et al. 2008). Although the urbanization process is a wide-spread, high-impact environmental transformation (Grimm et al. 2008), many studies show that cities host a surprisingly high number of species and individuals (e.g. Sukopp 1998; Marzluff 2001; Fernández-Juricic 2004; Palomino and Carrascal 2006). Moderately urbanized areas often support higher species richness than rural zones (Blair 1996; Blair and Launer 1997). Species richness and species diversity are generally considered good indicators of the quality of nature and ecosystem health (Rapport 1999). The importance of identifying thresholds of particular habitat variables which, if exceeded or undercut would cause biodiversity to be maintained or even enhanced in the urban environment, has been highlighted by several studies (e.g. Marzluff and Ewing 2001). Such predicted thresholds are important tools for convincing environmental managers and politicians of the effectiveness of specific measures. In addition, there is an increasing consensus that biodiversity is important for the quality of life of the people in general, and of urban inhabitants in particular. Sandström et al. (2006) claimed that perceived life quality of citizens might improve when the proportion of nature in urban areas increases. Conservation practices in cities give the opportunity for citizens to directly experience nature (Miller 2006), which is a crucial aspect for restoration in a world with a high urban population (Home et al. submitted).

Birds are often chosen as indicators of habitat quality. Their ecology is well known and species respond well to the availability of habitat structures (Dinetti et al. 1996; Luniak 1996; Clergeau et al. 1998). In cities, birds are widely considered as an optimal model group to study the ecological effect of urbanization (McDonnell and Hahs 2008). Strong inter-specific differences in the response of birds to urbanization are known (Blumstein et al. 2005;

Møller 2009), thus, it is expected that increasing urban densification modifies both bird community compositions and structure. Nevertheless, abiotic conditions are similar between cities (Grimm et al. 2008) and thus avian communities are often comparable, independent from latitude (Clergeau et al. 2006; Evans et al. 2009). The following general patterns have been identified on how urbanization influences avian biodiversity:

1) Bird species richness and diversity decrease along urbanization gradients ranging from moderately urbanized to densely built-up areas (Mirabella et al. 1996; Clergeau et al. 2006).
2) Avian abundance tends to increase along the same gradient (Clergeau et al. 1998; Palomino and Carrascal 2006; Grimm et al. 2008), which reflects the overall dominance of few synantrophic species (omnivorous and ubiquitous) that lead to biotic homogenization (e.g. Clergeau et al. 2006; Olden et al. 2006).
3) Specialist species (e.g. woodland and farmland species with narrow ecological requirements, often insect feeders and ground nesters) decrease with increasing urbanization (e.g. Clergeau et al. 1998; Fernández-Juricic 2004; Devictor et al. 2007).

Several studies provide evidence that site-specific environmental factors (< 1ha) influence avian species occurrence in urban areas (e.g. McKinney 2002; Sattler and Tobler 2004; Evans et al. 2009), which suggests that management decisions by inhabitants and property owners on the site scale can affect nesting and feeding habitats for urban birds (McKinney 2002; Grimm et al. 2008). The following management actions have been devised with the aim of enhancing urban bird populations: 1) providing additional food resources (Gaston et al. 2007; Evans et al. 2009) – 2) enhancing reproduction possibilities with nest boxes (Gaston et al. 2007) – 3) increasing structural vegetation diversity (Böhning-Gaese 1997; Chace and Walsh 2004; Tews et al. 2004; Evans et al. 2009), such as by providing a mixture of coniferous and deciduous woody plants (Thompson et al. 1993; Palomino and Carrascal 2006) – 4) planting native rather than exotic woody plants (Chace and Walsh 2004; Daniels and Kirkpatrick 2006; Burghardt et al. 2009) – 5) preserving woodland patches in urban developments (Croci et al. 2008) – 6) increasing connectivity among green structures within and around cities (Marzluff and Ewing 2001; Fernández-Juricic 2004).

Despite some knowledge on how these factors influence avian biodiversity (positively/negatively), there is an urgent need to know more about the effect size of single factors (Kim and Byrne 2006). These factors reflect past and present human management decisions (including planning) that affect biodiversity at a local scale in urban areas. Precise predictions of their effect sizes on species numbers and diversity facilitates the communication with policy makers and urban planners (e.g. McDonnell and Hahs 2008). The novelty of our study lays in this quantitative analysis of human-influenced factors to enhance bird species richness and diversity in the urban environment. The inclusion of broad aspects of human management allows direct comparisons of the effectiveness of the different measures under study. Often studies include only a few management variables in the analysis.

In an urban context, we expect that past planning and present management decisions on the site scale, such as individual gardens, exhibit a measurable influence on the avian community. We analyse and quantitatively predict the importance of the three urban aspects (i.e. structural elements, green composition, and green management) on avian species richness (species number) and diversity (representing species richness and evenness of a community, see Methods). For this purpose we chose three Swiss cities which are representative of small to medium sized cities in central Europe. In the beginning of this millennium in Switzerland, 73% of the population lived in cities (Schuler et al. 2004). In particular, we aim to answer the following questions:

A. Structural elements – Which are the most important urban elements that affect bird species richness and diversity?

B. Green composition – Which ratios of coniferous and deciduous trees and bushes, of native and exotic woody plant species and which number of woody plant species maximize bird species richness and diversity?

C. Green management – What is the influence of short- and long-term green management activities on bird species richness and diversity?

In addition to scientific information, this study provides necessary quantitative information for urban planners and managers so that decisions can be tailored to the enhancement of bird species richness and species diversity in cities.

3.3 Methods

3.3.1 Study sites and sampling design

We chose the three Swiss cities of Zurich, Lucerne (both North of the Alps) and Lugano (South of the Alps) for data collection (Table S1 in Supplementary material). The three cities consist of historical centres, residential areas, business quarters, public green areas, historical parks and cemeteries, and former industrial areas that have been developed for new apartments and office buildings. All three cities border a lake and are characterized by a temperate climate (North: average January temperature 1°C, July 17°C; South: January 3°C, July 20°C) with a yearly precipitation of 1000 mm for Zurich, 1150 mm for Lucerne and 1600 mm for Lugano.

In each of the three cities 32 sampling points were selected (total of 96) along continuous gradients of three habitat characteristics: 1) built and sealed area, 2) number of annual grass cuts and 3) age of the garden. Sampling points were selected to represent all possible combinations of these habitat characteristics (e.g. the combination of large proportion of built and sealed area, extensive management resulting from a low number of grass cuts and old urban structure is repeated in all cities).

A minimal distance of 250 m between sampling points inhibited spatial auto-correlation, which was confirmed using the Moran’s Index (Legendre and Legendre 1998; data not shown). The same minimal distance of 250 m was kept between sampling points and the city edge.

3.3.2 Bird survey

We applied the point count method in the early morning to record birds at sampling points (Bibby et al. 2000) during the breeding season (April 15th - June 13th 2007). Each of the 96 points was visited six times, over the two months (mean interval between visits: 10.6 days, range 4 – 15 days). Considering that the time of day affects bird activity, which in turn affects detection probability, the order of sampling points during one morning tour was alternated between start (one hour before sunrise) and finish (at the latest five hours after sunrise) of each tour. Each visit lasted 15 minutes to give a total of 6 x 15 = 90 minutes per sampling point (144 h overall). Presence of bird species was recorded visually and acoustically in a radius of 50 m, with the first 10 minutes of observations at the centre and the remaining 5 minutes checking areas hidden from the observer (e. g. behind buildings). When counting birds, we took special care that individuals were counted once only. We did not distinguish between breeders and other visitors, and over-flying birds were counted only when they were flying low and/or showed connection to the ground environment (i.e. searching for food). Species richness for each sampling point was defined as the total number of species detected during the six visits. Abundance for each species and sampling point was defined as the maximum number of individuals present in any of the six visits. We chose the Simpson index as measure of species diversity. The Simpson index emphasizes the evenness of a community, being less sensitive to species richness. It is meaningful, very robust, widely used and allows comparisons with the results of other studies (Magurran 2004):

$$Simpson = 1 - \sum_{i=1}^{n} {p_i}^2$$

where n is the number of species observed at the sampling point and p_i is the relative abundance of species i

3.3.3 Habitat variables

Eleven habitat variables were recorded at or within a 50 m radius of the count locations (Table 1). These explanatory variables were grouped into three categories according to the main research questions (see Introduction).

A) Structural elements – Detailed structural habitat variables were digitized using Geographic Information Systems (ArcGIS 9.2, ESRI Redlands, USA) and expressed as relative area coverage (100 % = 7854 m^2 for a single location).

B) Green composition – Two habitat variables are expressed as ratios (CONIFEROUS/DECIDUOUS and EXOTIC/NATIVE). We calculated mean species richness of woody plants (WOODY SPECIES RICHNESS), using the following formula:

$$WSR = \sum_{i=1}^{n} SR_i \cdot \frac{Area_i}{Area_{TOT}}$$

where n is the number of different woody plants patches within a 50 m radius, SR_i is the estimated number of woody plants species within patch i (three categories: 1 species (SR_i = 1), 2-3 species (= 2.5), ≥ 4 species (= 5)), $Area_i$ is the area of woody plants patch i and $Area_{TOT}$ is the total woody plants area within 50 m radius (sum of all $Area_i$).

C) Green management – We counted the number of cuts (CUTS) of the grass plots during regular visits over the whole vegetation period (26 weeks from mid-April to mid-October). The variable TRIMMED/UNTRIMMED is expressed as a ratio. We asked property owners to indicate the age of their green spaces (AGE), which is defined as the time since the last important structural modification or renewal of their garden and represents the management decision "not to replace old green structures with new ones".

3.3.4 Statistical analysis

We analysed the correlation of bird species richness and diversity with the habitat variables with linear mixed-effects models (Laird and Ware 1982; Crawley 2007), separating random effects (cities) from fixed effects (habitat variables). We found a normal distribution of the model residuals of both response variables (bird species richness and Simpson index) and thus used linear models.

We regressed species richness and species diversity (dependent variables) on the three different sets of explanatory variables as outlined in the paragraph on habitat variables and corresponding to the three study questions (A-C). All variables are continuous and were tested for pair-wise correlation. All correlation coefficients r were below 0.7 which we defined as the maximal accepted limit of correlation.

For each of the three analyses, we formulated a-priori models including all possible combinations of the variables. A total of 32 pre-defined models were tested for the structural elements analysis (question A) and eight models each for the woody plant composition (question B) and the management (question C) analysis. All composition models related to question B contained the area fraction of woody plants as a co-variable to account for the total cover at each sampling point. All management models related to question C contained the area fraction of TREE, BUSH and GRASS as co-variables. We expected curvilinear relations (optimum curves) for the variables CUTS and CONIFEROUS/DECIDUOUS (ratio), so we included their quadratic functions into the modeling for species richness and species composition. For the variable BUILDING we only expected a curvilinear relationship for the response variable bird species richness, because moderately built areas can host building dwelling species that profit from artificial rocks without necessarily losing the species already present at sampling locations with less buildings. On the other hand, for species diversity we expected BUILDING to exhibit a linear effect, as the Simpson index might be negatively affected by newly dominant building dwelling species. Consequently, we included the quadratic function of BUILDING into the modeling for species richness but not for species composition.

Models were ranked according to the small-sample unbiased Akaike's Information Criterion (AICc). AICc weights and evidence ratios were calculated (Burnham and Anderson 2002; Johnson and Omland 2004). Models with evidence ratios <10 were defined as the most parsimonious set of models. These selected models were predicted individually for all of the independent variables varying between the minimum and maximum value of the data set, while the remainder were kept constant at their mean value. By bootstrapping (1000 repetitions), standard deviations were calculated for the predicted values. Predicted values were then averaged based on their AICc weights (Burnham and Anderson 2002). The explained variation of every model was calculated using the generalized form of R2 for linear mixed effects models proposed by Xu (2003). All statistical calculations were carried out with the program R v2.6.0 (R Development Core Team 2007) using library nlme (Pinheiro et al. 2008).

3.4 Results

We recorded 5'441 observations of 63 species within a radius of 50 m from the 96 sampling points. Overall, we recorded an average of 15.2 species per sampling point (SD = 3.9; range = 7 – 25) with only small variation between the three cities (Table S1 in Supplementary material). For species identity and frequencies per city see Table S2.

3.4.1 Structural elements

For bird species richness, six out of the initial 32 models were defined as the most parsimonious set of models (Table 2, A). Their AICc weights sum to 92.7%. The explanatory power of the selected models is very high with an average R2 per selected model of 42.6%. The variable TREE is contained in all six selected models (sum of weights = 92.7%) and shows the highest positive correlation with bird species richness. SEALED AREA (five selected models; sum of weights = 81.4%) shows the highest negative correlation. BUSH and GRASS exhibit a moderately positive influence on bird species richness (three selected models each; sum of weights = 33.7% and 22.9%, respectively) while BUILDING (linear and quadratic term) shows a negative correlation with bird species richness (one selected model; weight = 7.9%).

For bird species diversity, nine out of the initial 32 models were defined as the most parsimonious set of models explaining the structural component analysis (Table 3, A). Their AICc weights sum to 87.0%. With an averaged R2 of 21.0%, their explanatory power is about half that of the models that explained species richness. Again, TREE is contained in eight of the nine selected models (sum of weights = 84.0%) and shows the highest positive correlation with species diversity. BUILDING shows a moderate negative correlation (four selected models; sum of weights = 23.4%), BUSH has a moderate positive correlation (three selected models; sum of weights = 25.4%), whereas there is hardly any correlation for GRASS and SEALED AREA (two selected models each; sum of weights = 13.8% and 9.5%, respectively).

The averaged predictions of these models (Fig. 1) illustrate the outstanding and positive influence of TREE on both bird species richness and diversity: a 20%-increase of tree area results in an average of three additional bird species and in an increase of Simpson index of about 0.24 (i.e. 24% increase in the probability that two randomly chosen birds belong to two different species). Evaluated by their standard deviations (SD), species richness predictions are reasonably reliable along the entire tree gradient under study, whereas the predictions for species diversity become less reliable for tree coverage above 30% of the total area. The variables BUSH and GRASS have a moderate and similar positive effect on bird species richness and diversity (although considerably less important than variable TREE). The predictions for SEALED AREA (Fig. 1) yield a contrasting picture for species richness (negative influence) and for species diversity (no influence). A 40%-increase of the sealed area causes a loss of three bird species, whereas predictions become less reliable when the proportion of sealed area is above 50%. In contrast to the influence of sealed area, species richness is not greatly influenced by the proportion of area covered by buildings, while a 25%-increase in built area decreases the Simpson index by about 0.01. In this case, species diversity predictions become less reliable for buildings fraction above 40%.

3.4.2 Green composition

For bird species richness, three models were defined as the most parsimonious set of models (Table 2, B) and their AICc weights sum to 95.9%. The explanatory power of these models, with the averaged R2 of 17.4%, is lower than in the analysis of the structural elements. The variable CONIFEROUS/DECIDUOUS (including its quadratic term) occurs in all the three selected models (sum of weights = 95.9%) and reveals a curvilinear response of bird species richness. The variables EXOTIC/NATIVE and WOODY SPECIES RICHNESS (one model each; weight = 25.7% and 8.6%, respectively) do not exhibit a strong influence on bird species richness.

For bird species diversity, three models were defined as the most parsimonious set of models (Table 3, B) and their AICc weights sum to 93.1%. The explanatory power of these models is very low with an averaged R2 of 0.5%. The best model is the null model (AIC weight = 71.3%) indicating random distribution (only the control variable total woody plants cover was included). Consequently, none of the analysed variables (CONIFEROUS/DECIDUOUS, EXOTIC/NATIVE and WOODY SPECIES RICHNESS) affects species diversity.

The averaged predictions of these models (Fig. 2) illustrate that only the variable CONIFEROUS/DECIDUOUS has a considerable (positive) influence on bird species richness. This variable shows a quadratic curve that probably has not yet reached its optimum. If all woody plants are deciduous, bird species richness is expected to be at its minimum value of about 14 species (= intercept). If deciduous and coniferous woody plants reach the same coverage (1:1 ratio), six additional bird species are predicted to be present. Predictions become less reliable for ratios > 1 and thus the prediction of the curve’s maximum becomes unreliable. Therefore we do not know whether a higher proportion of area covered by coniferous species would still increase bird species numbers. Bird species diversity does not respond to any variable included in the composition analysis (Fig. 2).

3.4.3 Green management

For bird species richness, six models were defined as the most parsimonious set of models (Table 2, C) and their AICc weights sum to 97.4%. The explanatory power of these models is low with an averaged R2 of 4.7%. The best model (weight = 40.9%) contains only the ratio variable TRIMMED/UNTRIMMED. This variable negatively correlates with bird species richness (three selected models; sum of weights = 52.1%). The second-best model consists of the null model (including only the control variables TREE, BUSH and GRASS) indicating that the chosen variables do not explain much of the variation in the data. Consequently, the variables CUTS (including its quadratic term) and AGE exhibit no influence on bird species richness.

For bird species diversity, three models were defined as the most parsimonious set of models (Table 3, C) and their AICc weights sum to 93.4%. Explanatory power of these models is very low with an averaged R2 of 1.6%. As the best model is the null model, none of the analysed variables (TRIMMED/UNTRIMMED, CUTS and AGE) influences species diversity.

The averaged predictions of these models (Fig. 3) illustrate that bird species richness is only negatively influenced by trimmed/untrimmed bushes ratio. If all bushes are untrimmed, bird species richness is at its maximum value of about 15 species (= intercept). If the ratio equals about 1:1, one bird species is lost. Predictions become less reliable for trimmed/untrimmed bushes ratios > 1. The influence of garden age on bird species diversity is faintly positive.

3.5 Discussion

3.5.1 Structural elements

Most studies on urban birds have considered the classical rural-urban gradient approach as proposed by McDonnell and Pickett (1990), which has generally shown a negative impact of urbanization (i.e. increased sealed area and building fraction) on bird species richness and diversity (e.g. Clergeau et al. 1998; Palomino and Carrascal 2006).

Our study, focusing on gradients within cities, confirmed the results of other authors in that urbanization also leads to homogenization of bird communities on this finer scale (Clergeau et al. 2006; Devictor et al. 2007; Sorace and Gustin 2008). At the same scale, the positive effect of amount and structural complexity of the urban green on the bird species richness and bird species diversity is consistent with the results of other studies (e.g. Böhning-Gaese 1997; Mason 2006; Shochat et al. 2006; Sorace and Gustin 2008). While sealed area decreases overall bird species richness, a dramatic reduction of bird diversity was observed with an increasing proportion of area covered by buildings. In highly urbanized areas, only few species (e.g. *Apus apus, Passer domesticus, Columba livia* f. *domestica*) profit from this anthropogenic secondary habitat (e.g. buildings as artificial rocks) and from abundant food resources, and thus dominate the community (Clergeau et al. 2006; McKinney 2006; La Sorte and McKinney 2007). Following the intermediate disturbance hypothesis (Connell 1978) and results of other studies (Blair 1996; Marzluff 2005; Tratalos et al. 2007), we expected bird species richness to attain its maximum at an intermediate ratio between buildings and urban green as a potential suitable mosaic in the urban matrix. However, our study revealed that buildings do not influence bird species richness, in that the loss of sensitive species is compensated by the appearance of generalist building dweller species (see species above).

3.5.2 Green composition

We confirm the positive influence of greater vegetation structures on bird species richness and diversity at the site scale (radius of 50 m), which corroborates previous studies (Emlen 1974; Lancaster and Rees 1979; Natuhara and Imai 1996; Clergeau et al. 2001; Sattler and Tobler 2004; Sorace and Gustin 2008). Our results suggest that the presence and amount of trees is the most important habitat variable enhancing bird species richness and diversity in cities, and thereby agree with other studies (Goldstein et al. 1986; Clergeau et al. 1998; Palomino and Carrascal 2006; Sandström et al. 2006; Evans et al. 2009). The positive effect of trees appears to outweigh the negative effect of sealed area and buildings by acting as an additional green layer to the urban matrix. The positive effect of both increasing bush and grass cover on bird richness and diversity is only moderate. As we chose height (5 m) to be the only criteria to discriminate between trees and bushes (neglecting plant habit) the great difference in the effect size between trees and bushes suggests that the additional vertical structure given by trees plays a key role in enhancing bird species richness and diversity. Therefore, increasing the proportion of tree cover in the urban matrix seems to be the most promising and efficient measure to enhance bird species richness and diversity. We predict an increase from 13 bird species in the absence of trees to 20 species with 46% of tree cover.

We found that tree composition is important for bird richness with the highest number of species expected when both coniferous and deciduous woody plants occur. In this way, bird species that rely on coniferous trees (i.e. *Parus ater, Parus cristatus, Regulus ignicapillus, Loxia curvirostra*) as well as others that rely on deciduous species (i.e. *Carduelis chloris, Muscicapa striata, Parus palustris, Phylloscopus collybita*) can coexist, thus maximizing the overall number of species, as indicated by Palomino and Carrascal (2006). To be more precise, our results indicate that the ratio of coniferous to deciduous trees and bushes should be at least 1:1 although predictions (Fig. 2) suggest the possibility that ratios >1:1 could enhance bird species richness even more. This result contradicts Thompson et al. (1993) who showed that bird species richness is highest in gardens with higher ratios of deciduous to coniferous trees.

With regard to the effect of native vs. exotic plants on birds, Daniels and Kirkpatrick (2006) found a higher correlation between native bird species and native plants than with exotic plants. In our study we found that the relative proportion of exotic and native woody plants does not influence bird species richness. In addition, our results show that woody plant species richness on the scale of the 50 m radius does not affect bird species richness. This finding contradicts the results of Shwartz et al. (2008), who found a positive influence of the number of woody plants species on avian species richness in urban areas, which was explained as being due to the increased structural complexity.

The lack of relationship observed in our study between any of the woody plant characteristics (e.g. coniferous vs. deciduous; exotic vs. native; plant species richness) and species diversity suggest that the absence of dominance of single bird species might be mainly determined by a high proportion of green area, in particular trees, as the most important habitat factor. Increasing sealed and built area induces few species to become dominant.

3.5.3 Green management

We found that the number of bird species decreases as the relative proportion of trimmed bushes increases, but the influence remains minor. The other short term management practice is the cutting frequency of the grass plot, which does not influence bird species richness. This finding is not surprising since both this study and that of Clergeau et al. (2006) found that ground nesting species are rare or even absent in cities. We measured the long-term management decisions “not to replace old green structure with new ones” and thereby allowing niches, structures, and complexity in the habitat to accumulate through time, and vegetations and structures of different ages to co-occur. Our results are consistent with Mason (2006) who found no correlation between the age of the habitat and bird species richness, whereas Clergeau et al. (1998) and Palomino and Carrascal (2006) showed that older settlements supported higher avian biodiversity.

In our study, bird diversity is not influenced by the short-term management methods of bush trimming or grass cutting. These variables do not affect the number of typically dominant species. The increasing garden age (long-term management) evokes a minimal positive influence of bird diversity (Fig 3).

3.5.4 Conclusions and perspectives

The requirement for more buildings and transport infrastructure puts high pressure on green space within cities (urban densification). To compensate for this loss of green area as habitats for birds in cities, we propose the promotion and shaping of vegetation structures that act positively on bird species richness and diversity. Based on the results of this study, we suggest two main quantitative recommendations that have effects on urban birds on which to base planning and management decisions and which can be applied even at our site scale of a 50 m radius. The first of these recommendations positively increases both bird richness and diversity, while the second measure maximizes bird species richness without showing an effect on diversity. Bird diversity seems to be quite robust to habitat changes once an increasing tree fraction has decreased the dominance of typically synantrophic species.

1) Planting trees and bushes (>5 m high) in order to optimize vertical vegetation structure is the best measure to enhance bird species richness and diversity. Our models predict an increase from 13 bird species in the absence of trees to 20 species with 46% of tree cover.
2) Ensure that there are at least as many coniferous woody plants as deciduous. Our models predict an increase from 14 bird species at places with the presence of only deciduous woody plants to 20 species at places where both coniferous and deciduous plants occur at a ratio of 1:1.

Avian species richness and diversity are two important components of bird biodiversity. However, they do not elucidate all aspects of urban bird dynamics and conservation. More than 60 bird species can breed in Swiss cities, which is approximately one third of all regularly breeding species of

Switzerland. Nevertheless Red List species (Keller 2001), priority species (Bollmann 2002) and specialists are underrepresented among the urban birds (Table S2). Thus, offering optimal habitats in cities cannot replace bird protection measures outside the city fringe (Miller 2006). Nevertheless, recent studies have shown the popularity of birds in the public (Home et al. In Press). So, urban birds and their diversity represent a crucial element on how people can experience urban nature. Such experiences are essential for a) the individual well-being of city inhabitants (Fuller et al. 2007), and b) for political decisions regarding environmental conservation since personal experiences influence people’s opinion (Turner et al. 2004).

Acknowledgments

Many people made this study possible. We would like to thank the BiodiverCity crew, namely M. Obrist and J. Ambrosini for their precious help. For technical and logistical support and precious scientific advices we acknowledge: B. Baur, R. Arlettaz, D. Cino, P. Duelli, T. Fabbro, F. A. Gebreselassie, M. Grüebler, G. and R. Guida, R. Home, D. Koller, P. Krebs, R. Lardelli, F. Maurer, B. Pezzatti, T. Roth, C. Sattler, M. Schaub, M. Weggler, N. Zbinden. The authorities of Lugano, Zurich and Lucerne with their corresponding contact institutions Dicastero del territorio & Dicastero servizi urbani Lugano, Grün Stadt Zürich, Naturförderung and Natur- und Landschaftsschutz, Umweltschutzamt Luzern for supporting the project. We are indebted to all inhabitants and owners who gave access to their proprieties. A special thank to D. Bajic and to the friends and family of S.F.

The present study is part of the project ‘BiodiverCity’ (www.biodivercity.ch) funded by the Swiss National Science Foundation in the framework of the National Research Program NRP54 ‘Sustainable development of the built environment’ (www.nrp54.ch).

3.6 References

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S., 2000. Bird Census Techniques. Academic Press, London.

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6, 506-519.

Blair, R.B., Launer, A.E., 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. Biological Conservation 80, 113-125.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. Journal of Applied Ecology 42, 943-953.

Böhning-Gaese, K., 1997. Determinants of avian species richness at different spatial scales. Journal of Biogeography 24, 49-60.

Bollmann, K., Keller, V., Müller, W., Zbinden, N., 2002. Prioritäre Vogelarten für Artenförderungsprogramme in der Schweiz. Der Ornithologische Beobachter 99, 301-320.

Burghardt, K.T., Tallamy, D.W., Shriver, W.G., 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conservation Biology 23, 219-224.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference – A Practical Information – Theoretic Approach. Springer-Verlag, New York.

Chace, J.F., Walsh, J.J., 2004. Urban effects on native avifauna: a review. Landscape and Urban Planning 74, 46-69.

Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M.L., Dinetti, M., 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. Biological Conservation 127, 336-344.

Clergeau, P., Jokimäki, J., Savard, J.P., 2001. Are urban bird communities influenced by the bird diversity of adjacent landscapes? Journal of Applied Ecology 38, 1122-1134.

Clergeau, P., Savard, J.-P., Mennechez, G., Falardeau, G., 1998. Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. Condor 100, 413-425.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302-1310.

Crawley, M.J., 2007. The R Book. John Wiley & Sons Ltd, Chichester.

Croci, S., Butet, A., Georges, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landscape Ecology 23, 1171-1186.

Daniels, G.D., Kirkpatrick, J.B., 2006. Does variation in garden characteristics influence the conservation of birds in suburbia? Biological Conservation 133, 326-335.

Devictor, V., Julliard, R., Couvet, D., Lee, A., Jiguet, F., 2007. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21, 741-751.

Dinetti, M., Cignini, B., Fraissenet, M., Zapparoli, M., 1996. Urban ornithological atlases in Italy. Acta Ornithologica 31, 15-23.

Emlen, J.T., 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. The Condor 76, 184-197.

Evans, K.L., Newson, S.E., Gaston, K.J., 2009. Habitat influences on urban avian assemblages. Ibis 151, 19-39.

Fernández-Juricic, E., 2004. Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain) – Implications for local and regional bird conservation. Landscape and Urban Planning 69, 17-32.

Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H., Gaston, K.J., 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3, 390-394.

Gaston, K.J., Fuller, R.A., Loram, A., MacDonald, C., Power, S., Dempsey, N., 2007. Urban domestic gardens (XI): variation in urban wildlife gardening in the United Kingdom. Biodiversity and Conservation 16, 3227-3238.

Goldstein, E.L., Gross, M., Degraaf, R.M., 1986. Breeding birds and vegetation: A quantitative assessment. Urban Ecology 9, 377-385.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., Briggs, J.M., 2008. Global change and the ecology of cities. Science 319, 756-760.

Home, R., Bauer, N., Hunziker, M., submitted. Psychosocial outcomes from contact with nature.

Home, R., Keller, C., Nagel, P., Bauer, N., Hunziker, M., In Press. Selection criteria for flagship species by conservation organizations. Environmental Conservation.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19, 101–108.

Keller, V., Zbinden, N., Schmid, H., Volet, B., 2001. Rote Liste der gefährdeten Brutvogelarten der Schweiz. Bundesamt für Umwelt, Wald und Landschaft (BUWAL) and Schweizerische Vogelwarte, Bern and Sempach.

Kim, K.C., Byrne, L.B., 2006. Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. Ecological Research 21, 794-810.

La Sorte, F.A., McKinney, M.L., 2007. Compositional changes over space and time along an occurrence-abundance continuum: anthropogenic homogenization of the North American avifauna. Journal of Biogeography 34, 2159-2167.

Laird, N.M., Ware, J.H., 1982. Random-Effects Models for Longitudinal Data. Biometrics 38, 963-974.

Lancaster, R.K., Rees, W.E., 1979. Bird communities and the structure of urban habitats. Canadian Journal of Zoology-Revue Canadienne De Zoologie 57, 2358-2368.

Legendre, P., Legendre, L., 1998. Numerical ecology, 2nd edn. Elsevier Science PV, Amsterdam.

Luniak, M., 1996. Inventory of the avifauna of Warsaw – species composition, abundance, and habitat distribution. Acta Ornithologica 31, 67-80.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Marzluff, J.M., 2001. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston.

Marzluff, J.M., 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8.

Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. Restoration Ecology 9, 280-292.

Mason, C.F., 2006. Avian species richness and numbers in the built environment: can new housing developments be good for birds? Biodiversity and Conservation 15, 2365-2378.

McDonnell, M.J., Hahs, A.K., 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23, 1143-1155.

McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban rural gradients: an unexploited opportunity for ecology. Ecology 71, 1232-1237.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. Bioscience 52, 883-890.

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127, 247-260.

Miller, J., 2006. Restoration, reconciliation, and reconnecting with nature nearby. Biological Conservation 127, 356-361.

Mirabella, P., Fraissenet, M., Milone, M., 1996. Breeding birds and territorial heterogenity in Naples city (Italy). Acta Ornithologica 31, 25-31.

Møller, A.P., 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159, 849-858.

Natuhara, Y., Imai, C., 1996. Spatial structure of avifauna along urban-rural gradients. Ecological Research 11, 1-9.

Olden, J.D., Poff, N.L., McKinney, M.L., 2006. Forecasting faunal and floral homogenization associated with human population geography in North America. Biological Conservation 127, 261-271.

Palomino, D., Carrascal, L.M., 2006. Urban influence on birds at a regional scale: A case study with the avifauna of northern Madrid province. Landscape and Urban Planning 77, 276-290.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2008. nlme: Linear and Nonlinear Mixed Effects Models.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rapport, D.J., 1999. Perspectives on ecological integrity. Environmental Values 8, 116-118.

Sandström, U.G., Angelstam, P., Mikusinski, G., 2006. Ecological diversity of birds in relation to the structure of urban green space. Landscape and Urban Planning 77, 39-53.

Sattler, T., Tobler, M., 2004. Development of breeding populations of birds in two residential areas in Solothurn and their dependence on habitat structure – Bestandsentwicklung und Strukturabhängigkeit von Brutvögeln in zwei Wohnquartieren der Stadt Solothurn (in German with English summary). Der Ornithologische Beobachter 101 177-192.

Schuler, M., Perlik, M., Pasche, N., 2004. Nicht-städtisch, rural oder peripher – wo steht der ländliche Raum heute? ARE, Bundesamt für Raumentwicklung, Bern.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21, 186-191.

Shwartz, A., Shirley, S., Kark, S., 2008. How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? Landscape and Urban Planning 84, 219-229.

Sorace, A., Gustin, M., 2008. Homogenisation processes and local effects on avifaunal composition in Italian towns. Acta Oecologica-International Journal of Ecology 33, 15-26.

Sukopp, H., 1998. Stadtökologie – Ein Fachbuch für Studium und Praxis. Fischer, Stuttgart.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79-92.

Thompson, P.S., Greenwood, J.J.D., Greenaway, K., 1993. Birds in European gardens in the winter and spring of 1988-89. Bird Study 40, 120-134.

Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D., Gaston, K.J., 2007. Bird densities are associated with household densities. Global Change Biology 13, 1685-1695.

Turner, W.R., Nakamura, T., Dinetti, M., 2004. Global urbanization and the separation of humans from nature. Bioscience 54, 585-590.

United Nations, 2008. World Urbanization Prospects: the 2007 Revision. United Nations, New York.

Xu, R.H., 2003. Measuring explained variation in linear mixed effects models. Statistics in Medicine 22, 3527-3541.

3.7 Tables and figures

Table 1: Habitat variables grouped in three categories according to the main study questions A-C. All variables are continuous.

Category	Variable	Mean (min-max)	Unity	Definition
A) Structural elements	BUILDING	0.23 (0-0.65)	Relative coverage in radius 50m	Buildings
	SEALED AREA	0.26 (0-0.78)		Asphalted surfaces (roads, spots), diverse anthropogenic features (i.e. gazebos, statues, fountains)
	GRASS	0.30 (0.03-0.76)		Short grass, long grass and native flowers
	BUSH	0.13 (0-0.36)		Woody plants (< 5m high)
	TREE	0.13 (0-0.47)		Woody plants (> 5m high)
B) Green composition	CONIFEROUS/ DECIDUOUS	0.25 (0-2.91)	Ratio	Coniferous/deciduous woody plants cover ratio (trees and bushes)
	EXOTIC/ NATIVE	1.95 (0-13.93)		Exotic/native woody plants cover ratio (trees and bushes)
	WOODY SPECIES RICHNESS	2.14 (1-4.54)	n	Mean number of woody plants species
C) Green management	CUTS	6 (0-20)	n	Number of cuts of the grass plot during vegetation period
Short-term management	TRIMMED/ UNTRIMMED	0.40 (0-2.25)	Ratio	Trimmed/untrimmed bushes cover ratio
Long-term management	AGE	42 (2-157)	years	Age of the garden since the last important structural modification or renewal of the green area[1]

[1] Information obtained from the inhabitants/owners

Table 2: Linear mixed-effects models relating species richness to environmental variables. Estimates (± SD), Δ-AICc (difference compared to small-sample unbiased Akaike's Information Criterion of the best model), AICw (model weight), ER (evidence ratio), k (number of parameters) and adjusted R2 (Xu 2003) are shown for every model having ER smaller than 10 (most parsimonious set of models). A) Structural elements analysis; B) Green composition analysis; C) Green management analysis.

A)	**Model**	**Intercept**	**Tree**	**Bush**	**Grass**	**Sealed area**	**Building**	**Building^2**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
	8	15.6 (± 1.0)	16.3 (± 3.2)			-9.7 (± 2.4)			0	45.0%	1	5	41.3%
	17	14.6 (± 1.2)	15.8 (± 3.2)	6.4 (± 4.3)		-8.8 (± 2.4)			2.0	17.0%	2.7	6	42.6%
	16	9.5 (± 1.0)	12.7 (± 3.6)	13.2 (± 4.2)	7.6 (± 2.2)				2.8	11.3%	4.0	6	42.0%
	21	17.7 (± 1.7)	11.3 (± 4.0)			-9.7 (± 2.3)	-5.8 (± 8.6)	-3.2 (± 14.8)	3.5	7.9%	5.7	7	44.3%
	19	15.0 (± 1.5)	15.5 (± 3.5)		1.5 (± 2.7)	-8.7 (± 3.0)			4.0	6.2%	7.3	6	41.5%
	26	12.4 (± 2.0)	13.4 (± 3.6)	9.5 (± 4.8)	4.2 (± 3.0)	-5.6 (± 3.4)			4.3	5.4%	8.4	7	43.7%

B)	**Model**	**Intercept**	**Coniferous / Deciduous**	**(Coniferous / Deciduous)^2**	**Exotic / Native**	**Woody species richness**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
	1	10.2 (± 0.8)	6.0 (± 1.9)	-1.1 (± 0.8)			0	61.6%	1	6	16.1%
	4	10.7 (± 0.9)	6.6 (± 1.9)	-1.3 (± 0.8)	-0.2 (± 0.1)		1.8	25.7%	2.4	7	19.9%
	5	9.6 (± 1.2)	6.3 (± 2.0)	-1.2 (± 0.8)		0.3 (± 0.5)	3.9	8.6%	7.2	7	16.3%

C)	**Model**	**Intercept**	**Trimmed / untrimmed**	**Cuts**	**Cuts^2**	**Age**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
	2	10.7 (± 1.1)	-1.4 (± 0.6)				0	40.9%	1	7	5.4%
	0	9.5 (± 1.0)					0.5	32.0%	1.3	6	0.0%
	3	9.1 (± 1.0)				0.01 (± 0.01)	3.4	7.4%	5.5	7	1.5%
	6	10.3 (± 1.2)	-1.3 (± 0.7)			0.01 (± 0.01)	3.6	6.8%	6.0	8	6.2%
	1	10.4 (± 1.2)		-0.4 (± 0.2)	0.03 (± 0.01)		3.9	5.9%	7.0	8	5.4%
	4	11.2 (± 1.2)	-1.3 (± 0.7)	-0.3 (± 0.2)	0.02 (± 0.01)		4.5	4.4%	9.3	9	9.5%

Table 3: Linear mixed-effects models relating species diversity to environmental variables. Estimates (± SD), Δ-AICc (difference compared to small-sample unbiased Akaike's Information Criterion of the best model), AICw (model weight), ER (evidence ratio), k (number of parameters) and adjusted R2 (Xu 2003) are shown for every model having ER smaller than 10 (most parsimonious set of models). A) Structural elements analysis; B) Green composition analysis; C) Green management analysis.

A)

Model	**Intercept**	**Tree**	**Bush**	**Grass**	**Sealed area**	**Building**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
1	0.81 (± 0.01)	0.28 (± 0.06)					0.0	28.4%	1.0	4	19.4%
6	0.80 (± 0.02)	0.26 (± 0.06)	0.14 (± 0.08)				1.3	14.9%	1.9	5	21.6%
9	0.85 (± 0.03)	0.20 (± 0.07)				-0.11 (± 0.07)	1.5	13.4%	2.1	5	21.8%
7	0.80 (± 0.02)	0.23 (± 0.07)		0.05 (± 0.04)			2.7	7.3%	3.9	5	20.7%
8	0.83(± 0.02)	0.25 (± 0.06)			-0.05 (± 0.05)		2.9	6.6%	4.3	5	20.4%
16	0.78 (± 0.02)	0.20 (± 0.07)	0.16 (± 0.08)	0.07 (± 0.04)			3.0	6.5%	4.4	6	23.7%
18	0.83 (± 0.03)	0.20 (± 0.07)	0.11 (± 0.08)			-0.09 (± 0.07)	3.9	4.0%	7.1	6	23.0%
5	0.90 (± 0.02)					-0.22 (± 0.05)	4.5	3.0%	9.3	4	15.7%
21	0.86 (± 0.03)	0.18 (± 0.08)			-0.05 (± 0.05)	-0.11 (± 0.07)	4.5	2.9%	9.7	6	22.7%

B)

Model	**Intercept**	**Coniferous / Deciduous**	**(Coniferous / Deciduous)^2**	**Exotic / Native**	**Woody species richness**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
0	0.79 (± 0.02)					0.0	71.3%	1.0	4	0.0%
2	0.80 (± 0.02)			0.00 (± 0.00)		3.6	11.6%	6.2	5	0.9%
3	0.80 (± 0.02)				-0.01 (± 0.01)	3.9	10.3%	6.9	5	0.6%

C)

Model	**Intercept**	**Trimmed / untrimmed**	**Cuts**	**Cuts^2**	**Age**	**Δ-AICc**	**AICw**	**ER**	**k**	**R^2**
0	0.78 (± 0.02)					0.0	54.9%	1.0	6	0.0%
3	0.77 (± 0.02)				0.00 (± 0.00)	1.5	26.3%	2.1	7	3.1%
2	0.79 (± 0.02)	-0.01 (± 0.01)				3.0	12.2%	4.5	7	1.6%

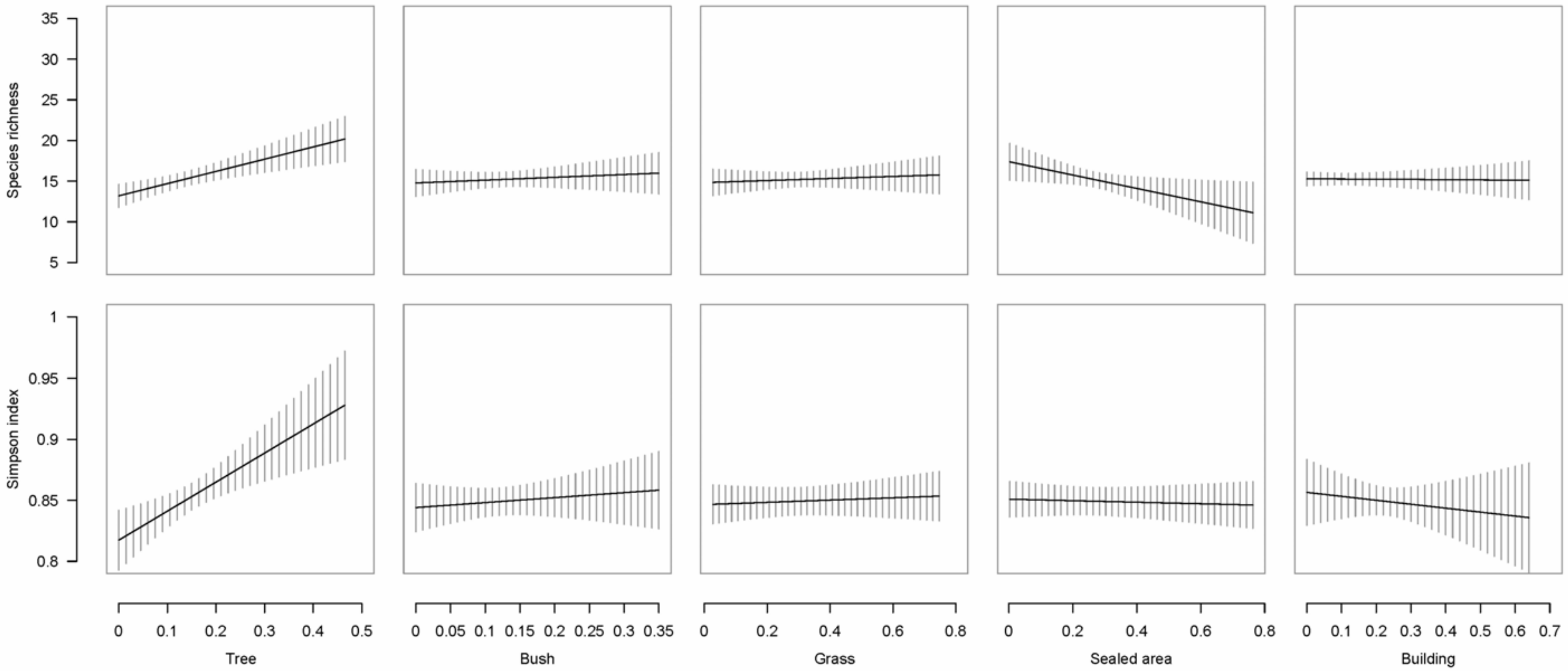

Fig. 1: Model averaged predictions (mean ± SD) of bird species richness (above) and bird species diversity (below) based on the most parsimonious set of models for structural elements analysis.

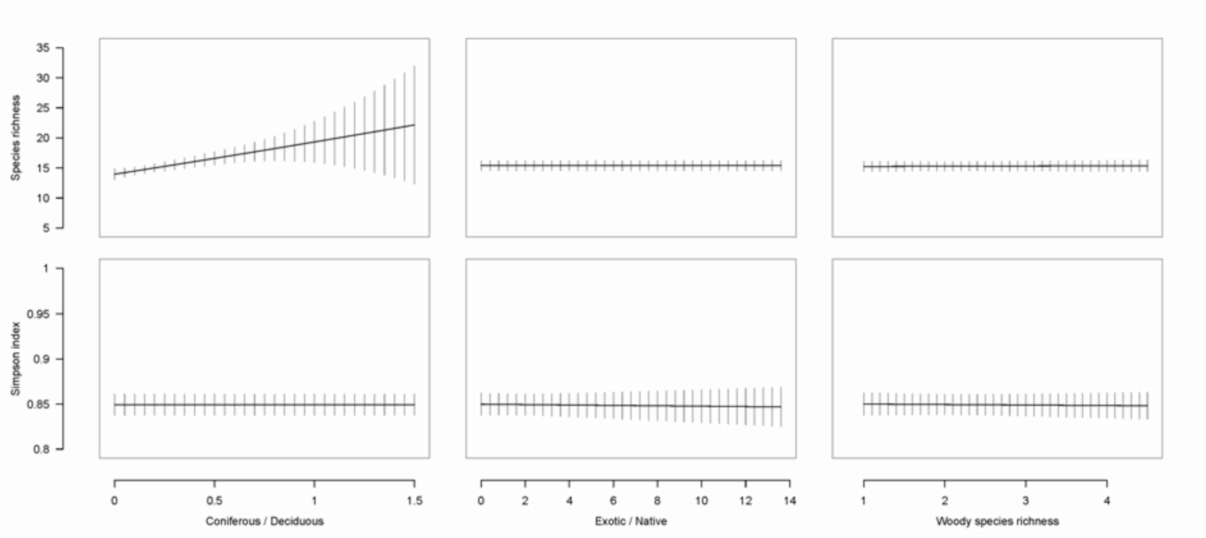

Fig. 2: Model averaged predictions (mean ± SD) of bird species richness (above) and bird species diversity (below) based on the most parsimonious set of models for green composition analysis.

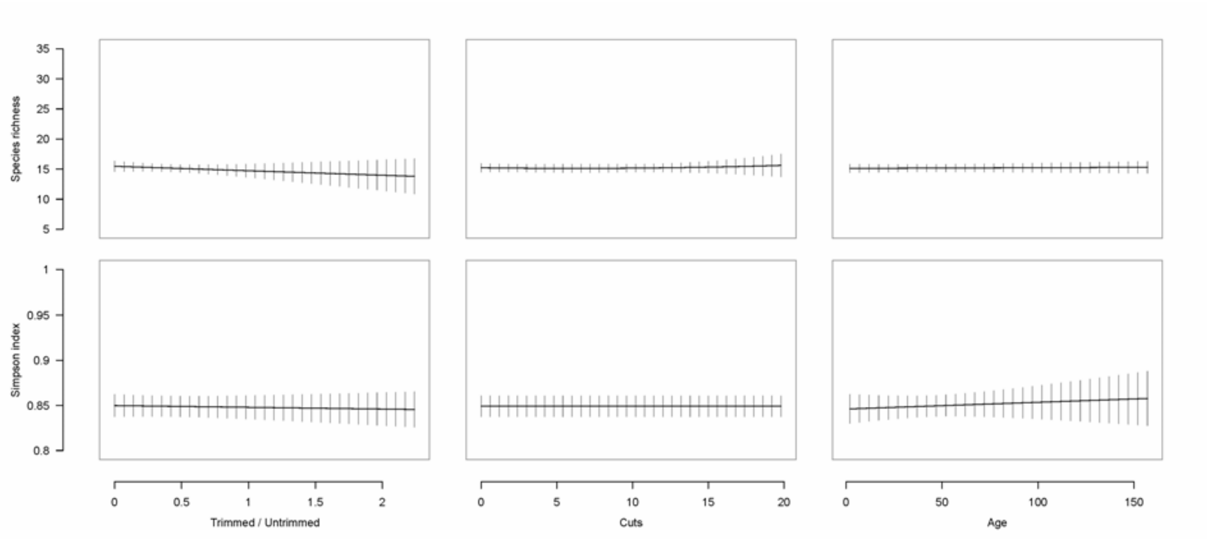

Fig. 3: Model averaged predictions (mean ± SD) of bird species richness (above) and bird species diversity (below) based on the most parsimonious set of models for green management analysis.

3.8 Supplementary material

Table S1: Information according to the three study cities: a) information on location, geographical extent and human population; b) bird species richness in the three cities (total, mean, range).

	Zurich	**Lucerne**	**Lugano**
a)			
Geographical coordinates	47°22′N 8°33′E	47°03′N 8°18′E	46°00′N 8°57′E
Area	91.88 km²	24.15 km²	26.2 km²
Elevation	408 m a.s.l.	436 m a.s.l.	273 m a.s.l.
Residents	367’000	58’000	49'000
b)			
Total bird species richness	42	51	40
Mean (± SD) per sampling point	14.0 (± 3.7)	16.4 (± 4.4)	15.1 (± 3.2)
Range	9-25	9-25	7-21

Table S2: Bird species according to the three study cities (n locations = 32 per city, total 96). Steadiness expresses the number of sampling points with the presence of the species. Dominance indicates the fraction (%) of individuals of a single species on the total individual number of birds.

Conservation status according to the Red List of birds of Switzerland (Keller 2001): VU = Vulnerable, NT = Near Threatened; # = indicates whether a species was considered as a priority species for Switzerland (Bollmann 2002); § identifies indicator species for urban habitats (Zbinden et al. 2005).

Scientific name	**Species status**	**Zurich: steadiness and dominance (%)**	**Lucerne: steadiness and dominance (%)**	**Lugano: steadiness and dominance (%)**	**Overall: steadiness and dominance (%)**
Accipiter nisus		1 (0.1)	1 (0.1)	0 (0.0)	2 (0.0)
Acrocephalus scirpaceus		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Aegithalos caudatus		5 (0.9)	14 (2.3)	10 (1.9)	29 (1.7)
Anas platyrhynchos		1 (0.1)	5 (0.8)	0 (0.0)	6 (0.3)
Apus apus	#, §	28 (18.4)	29 (12.2)	25 (7.0)	82 (12.4)
Apus melba	NT, #	2 (0.4)	2 (0.7)	1 (0.1)	5 (0.4)
Ardea cinerea		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Buteo buteo		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Carduelis cannabina		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Carduelis carduelis	§	15 (1.7)	19 (2.5)	25 (3.7)	59 (2.7)
Carduelis chloris	§	30 (4.6)	26 (3.1)	30 (4.5)	86 (4.1)
Certhia brachydactyla		4 (0.3)	5 (0.4)	2 (0.1)	11 (0.3)
Coccothraustes coccothraustes		1 (0.1)	0 (0.0)	0 (0.0)	1 (0.0)
Columba livia f. *domestica*		12 (3.3)	8 (1.8)	22 (5.6)	42 (3.6)
Columba palumbus		3 (0.2)	10 (1.0)	0 (0.0)	13 (0.4)
Corvus corone		28 (4.9)	28 (5.0)	32 (6.9)	88 (5.6)
Corvus monedula	VU, #	1 (0.3)	5 (0.7)	0 (0.0)	6 (0.3)
Delichon urbica	§	1 (0.1)	0 (0.0)	9 (2.4)	10 (0.8)
Dendrocopos major		7 (0.6)	7 (0.6)	2 (0.1)	16 (0.4)
Emberiza cirlus	VU, #	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)

Erithacus rubecula		12 (1.1)	11 (0.9)	14 (1.2)	37 (1.1)
Fringilla coelebs		26 (3.6)	30 (4.8)	28 (3.7)	84 (4.1)
Garrulus glandarius		3 (0.4)	5 (0.5)	0 (0.0)	8 (0.3)
Hippolais polyglotta	NT	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Hirundo rustica		1 (0.2)	1 (0.1)	4 (0.4)	6 (0.2)
Jynx torquilla	VU, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Larus michahellis	NT	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Locustella naevia	VU, #	0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Loxia curvirostra		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Mergus merganser	VU	0 (0.0)	2 (0.1)	0 (0.0)	2 (0.0)
Milvus migrans		2 (0.2)	2 (0.2)	0 (0.0)	4 (0.1)
Motacilla alba		7 (0.7)	10 (1.0)	11 (0.9)	28 (0.9)
Muscicapa striata	§	7 (0.6)	15 (1.5)	10 (1.0)	32 (1.0)
Oenanthe oenanthe		0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Parus ater		3 (0.2)	6 (0.6)	7 (0.7)	16 (0.5)
Parus caeruleus		28 (3.9)	26 (4.3)	16 (1.4)	70 (3.2)
Parus cristatus		0 (0.0)	2 (0.2)	0 (0.0)	2 (0.1)
Parus major		29 (5.9)	32 (6.4)	24 (3.0)	85 (5.1)
Parus palustris		1 (0.1)	3 (0.3)	0 (0.0)	4 (0.1)
Passer domesticus	§	32 (24.1)	29 (16.7)	0 (0.0)	93 (23.5) *
Passer hispaniolensis italiae	§	0 (0.0)	0 (0.0)	32 (29.4)	
Passer montanus		1 (0.2)	1 (0.1)	2 (0.4)	4 (0.2)
Phalacrocorax carbo		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Phoenicurus ochruros		19 (1.8)	28 (3.3)	14 (1.2)	61 (2.1)
Phoenicurus phoenicurus	NT, #	2 (0.2)	1 (0.1)	18 (1.8)	21 (0.7)
Phylloscopus collybita		5 (0.5)	10 (0.9)	2 (0.1)	17 (0.5)
Phylloscopus trochilus	NT, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Pica pica		19 (2.3)	11 (1.4)	0 (0.0)	30 (1.2)
Picus viridis		1 (0.1)	1 (0.1)	2 (0.1)	4 (0.1)
Ptyonoprogne rupestris		0 (0.0)	0 (0.0)	2 (0.4)	2 (0.1)
Pyrrhula pyrrhula		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)
Regulus ignicapillus		6 (0.6)	15 (1.6)	9 (0.8)	30 (1.0)
Regulus regulus		1 (0.2)	0 (0.0)	0 (0.0)	1 (0.0)
Saxicola rubetra	NT, #	0 (0.0)	0 (0.0)	1 (0.1)	1 (0.0)
Serinus serinus	§	8 (0.6)	15 (1.5)	24 (2.7)	47 (1.6)

Sitta europaea		8 (0.7)	10 (1.0)	7 (0.6)	25 (0.8)
Streptopelia decaocto	§	14 (1.9)	5 (0.6)	19 (2.7)	38 (1.7)
Sturnus vulgaris		20 (3.4)	19 (3.3)	10 (1.4)	49 (2.7)
Sylvia atricapilla		21 (3.2)	27 (3.3)	28 (4.8)	76 (3.8)
Troglodytes troglodytes		3 (0.4)	5 (0.4)	4 (0.4)	12 (0.4)
Turdus merula		31 (7.1)	32 (12.5)	31 (8.1)	94 (9.2)
Turdus philomelos		0 (0.0)	2 (0.1)	0 (0.0)	2 (0.0)
Turdus viscivorus		0 (0.0)	1 (0.1)	0 (0.0)	1 (0.0)

* As Passer hispaniolensis italiae substitutes P. domesticus in Lugano, we calculate the overall steadiness and dominance as if they were the same species.

References cited in supplementary material

Bollmann K., Keller, V., Müller, W., Zbinden, N. 2002. Prioritäre Vogelarten für Artenförderungsprogramme in der Schweiz. Der Ornithologische Beobachter 99: 301-320.

Keller V., Zbinden, N., Schmid, H., Volet, B. 2001. Rote Liste der gefährdeten Brutvogelarten der Schweiz. Bundesamt für Umwelt, Wald und Landschaft (BUWAL) and Schweizerische Vogelwarte, Bern and Sempach.

Zbinden N., Schmid H., Kéry M. and Keller V. 2005. Swiss Bird Index SBI® – Kombinierte Indices für die Bestandsentwicklung von Artengruppen regelmässig brütender Vogelarten der Schweiz 1990–2004. Der Ornithologische Beobachter 102: 283-291.

4

Arthropod and bird communities in cities: shaped by environmental control and high stochasticity

Arthropod and bird communities in cities: shaped by environmental control and high stochasticity

T. Sattler[1, 2], D. Borcard[3], R. Arlettaz[2], F. Bontadina[2], P. Legendre[3], M.K. Obrist[4], M. Moretti[1, 3]

[1] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[2] Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[3] Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

[4] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

Foreseen Journal: *Ecology*

4.1 Abstract

Spatially organized distribution patterns of species and communities are shaped by both autogenic spatial processes reflecting neutral mechanism theory and exogenous spatial processes reflecting niche theory. In the latter, environmental variables that are themselves spatially organized cause spatial structure. The relative importance of these processes has not yet been investigated in urban habitats. We used variation partitioning to compare the relative fractions of explained variance by purely spatial, spatially structured environmental and purely environmental components for the community composition of spiders (Araneae), bees (Apidae) and birds (Aves) at 96 locations in three Swiss cities. Environmental variables (topographic, climatic, habitat cover, management) were measured on four different radii (local, 50m, 250m, 1000m), while spatial variables were obtained from spatially weighted connectivity matrices, called Moran's eigenvector maps (MEMs). We identified very limited fractions of explained variance by purely spatial or by spatially structured environmental components in all three taxonomical groups. The results indicate that human influence in urban areas has disrupted spatially structured environmental variables and inhibits the development of biotic spatial processes. We suggest that the near absence of spatial structure is a feature typical of urban species assemblages and that urban community composition is mainly influenced by environmental variables. Spider communities react to very fine-scaled environmental changes of management and climate. Bird community composition is determined by woody plant as well as solar radiation variables at all radii, and different bird species are likely to be affected by environmental variables measured on different scales. Bee communities were explained with single variables only and low fractions of total explained variance were obtained. Urban environments represent a close-knit mosaic of habitats which are regularly disturbed. Species communities in urban areas are far from equilibrium and need to be considered as being in constant change to adopt to disturbances and changes imposed by human activities. These circumstances favor generalist species that use a variety of habitat types and that are not limited by the fragmented nature of urban habitats.

Keywords

Araneae, Spiders, Apidae, Bees, Aves, Birds, Switzerland, Beta diversity, Disturbance, Built environment, Cities, Urban

4.2 Introduction

Identification of the factors and underlying processes explaining species distribution by means of environmental and spatial models are vividly discussed ecological topics (e.g. Legendre 1993, Koenig 1999, Wagner 2003, Legendre et al. 2005, Legendre et al. 2009). The spatial processes shaping community composition generally pertain to two sources (Legendre 1993, Legendre and Legendre 1998, Fortin and Dale 2005): (1) Autogenic spatial structure is generated by biotic processes such as dispersal, growth, mortality, interspecific competition or predation. The neutral theory of biodiversity (Bell 2000, Hubbell 2001) predicts that such processes lead to spatial autocorrelation, which can be assessed as a pure spatial component using variation partitioning (Borcard and Legendre 2002, Borcard et al. 2004). (2) Exogenous spatial structure stems from the classical environmental control model by selection of the species' ecological niche (Hutchinson 1957) and arises when species respond to environmental variables that are themselves spatially structured. This is sometimes called spatially structured or induced environmental dependence (Borcard and Legendre 2002, Borcard et al. 2004). It is challenging to disentangle the relative contributions of these processes, and to determine the scales at which they are operating (Borcard and Legendre 1994, Jones et al. 2008). However, it is essential to measure environmental variables at the relevant spatial extent (local, meso, landscape) for the focal taxa (Duelli 1997, Luoto et al. 2007, Jombart et al. 2009). Habitat cover is often measured in concentric rings of different radii and examined with circular analysis (e.g. Steffan-Dewenter et al. 2002, Pellet et al. 2004). To measure the spatial component, Borcard and Legendre (2002) and Borcard et al. (2004) recently introduced Principal Coordinates of Neighbor Matrices (PCNM) and Dray et al. (2006) developed the more general Moran's eigenvector maps (MEMs). PCNM variables actually form a sub-family of the MEM variables with both being eigenvectors obtained from spatially weighted connectivity matrices of sampling locations.

Relationships between communities and both environmental and spatial variables are assessed with canonical ordination methods, especially redundancy analysis (RDA; Rao 1964). Variation partitioning disentangles the relative importance of unique and shared effects of different explaining data sets (Borcard et al. 1992, Borcard and Legendre 1994, Legendre et al. 2005). The obtained ecological information is important for the basic ecological knowledge of species or communities (Böhning-Gaese 1997, Cushman and McGarigal 2002) as well as for judging the effectiveness of (potential) conservation measures (Betts et al. 2006, Kivinen et al. 2007, Johnston et al. 2008). Variation partitioning lends itself to the study of complex ecosystems.

Urban areas are ecosystems (Sukopp 1998) that are characterized by a unique environmental complexity, which is often referred to as the 'urban mosaic' (Rebele 1994, Sattler et al. submitted). Variation partitioning, however, has rarely been applied in this environment to investigate the relative contributions of different components affecting species communities. Species composition in the close-knit urban matrix may be influenced by the availability of many, often fine-scaled habitat types (e.g. trees, meadow, bushes, ornamental plants, gardens, lawns etc.), built structures (buildings, sealed areas), regional effects, topography, climate (Urban Heat Island effect; Pickett et al. 2001), pollution, and traffic. Current knowledge of species distributions in urban environments is often based on studies dealing with single taxa at a single spatial scale (Palomino and Carrascal 2006, Devictor et al. 2007). This limits our understanding of how environmental and spatial factors interact and affect community composition at different scales.

In our study, we address the following questions: A) Which environmental variables measured on which radius explain best community composition of spiders, bees and birds in urban areas? B) How much of the variation in community composition is explained by four environmental data sets (measured at local, 50m, 250m, and 1000m radii) individually, or in combinations? C) Finally, what is the relative importance of the purely environmental (PE), the spatially structured environmental (SSE) and the purely spatial (PS) components on local community composition? With this last question, which to our knowledge has not yet been addressed for urban environments in any taxonomic group, we identify the processes (niche, neutral) that best explain the observed community composition.

4.3 Methods

4.3.1 Study sites and sampling design

Data were collected in the three Swiss cities of Lucerne, Zurich (both North of the Alps) and Lugano (South of the Alps), representative for small to medium sized European cities (53'000-371'000 inhabitants) of central European lowlands (273-436m asl). All three cities are characterised by historical centres, residential areas including old gardens, parks and cemeteries (often > 100 years), business quarters and former but discontinued industrial areas, which are transformed for new purposes. They experience a temperate climate (North: average January temperature 1°C, July 17°C; South: January 3°C, July 20°C).

We selected three taxonomic groups that we expected to respond to environmental variables at different spatial scales: spiders (Araneae), bees (Apidae) and birds (Aves). Community composition of all three species groups (birds, bees, spiders) was surveyed at the same 32 study locations in each city to give a total number of 96 study locations. For each city, we selected sampling locations along three gradients, namely 'age of green area', 'impervious area', and 'management intensity of the meadow/lawn plots'. We chose a non representative reasoned choice sampling strategy to maximize variation along these main gradients, including all possible combinations of minimum and maximum values. Results must only be interpreted within the range of these gradients (values see below). The study locations included private gardens, semi-public spaces between apartment buildings, public parks, and courtyards of industrial buildings (detailed locations in Germann et al. 2008).

4.3.2 Arthropod sampling

At each of the 96 study locations, surface dwelling arthropods were sampled using three pitfall traps (cups) and flying invertebrates were sampled using combination traps (Duelli et al. 1999). Arthropods were caught during seven weeks in the period of highest species richness in Central Europe (Duelli et al. 1999). Traps were opened between June 13th and 15th 2006 (depending on cities) and then emptied weekly until closure between August 1st and 3rd 2006. Bees and spiders were sorted from the remaining arthropods and identified and counted by specialists (see acknowledgements). Juvenile spiders, as their determination at species level is not reliable, and the European honey bee (*Apis mellifera*), since the occurrence of this bred species mainly depends on the distribution of the bee keepers, were excluded from the analysis. More information on arthropod sampling is included in Sattler et al. (submitted).

4.3.3 Birds survey

We applied the point count method in the early morning (Bibby et al. 2000) to record birds at the same sampling points as the arthropods Each of the 96 points was visited six times between April 15th to June 13th 2007 (corresponding to the breeding season) and bird species were surveyed visually and acoustically within a radius of 50m for 15 minutes. The observer stayed in the central point for the initial 10 minutes and checked hidden areas, such as behind buildings in the last 5 minutes. Since the time of day affects bird activity, which in turn affects detection probability, the order of sampling points was alternated between start and end of each tour. Over-flying birds were counted only when they showed connection to the ground environment (i.e. searching for food). More details on bird survey are found in Fontana et al. (submitted).

4.3.4 Environmental predictors

An overview on the four data sets used as environmental variables is presented in Table 1. The data set 'local' consists of six topographical variables and four variables describing additional local conditions. The topographical variables labeled Slope, Eastness trap, and Northness trap were measured directly at the sampling location while the variables labeled Elevation, Eastness hillside, and Northness hillside were obtained from a Digital Elevation Model. The additional variables were labeled Age, Management intensity, Soil density, and Sun exposure. We asked property owners to indicate the age of their green spaces, which we defined as the time since the last important structural modification or renewal of the green area. We counted the number of cuts of the grass or meadow plots during regular visits over the whole vegetation period (26 weeks from mid-April to mid-October) to determine management intensity. Soil density and Sun exposure were measured at each sampling location. The other three environmental data sets were measured as a circular analysis of three different radii around the sampling points (data sets on 50m radius (R50m), on 250m radius (R250m), and on 1000m radius (R1000m)). Land cover variables, labeled Agriculture, Roads, and Urban Green, were measured as frequencies (%) obtained from theme-specific layers of the topographic map 1:25’000 of Switzerland. Agriculture was not included in the R50m, as few locations featured this variable within this radius. The land cover type ‘building’ was not included in the analysis as it correlated with other variables ($r>0.7$).

Digital Surface Models for Switzerland depict the elevation of the Earth's surface including vegetation and buildings (Artuso et al. 2003) using airborne laser scanning methods. These data are available in cell sizes of 2.5 x 2.5m and have an accuracy of ±0.5 m in open terrain ±1.5 m in terrain with vegetation. We used the module ‘Area Solar radiation’ of ArcMap 9.3 (ESRI Inc., Redlands, USA) to calculate solar radiation (expressed in Watt hours/m^2) for all cells. Shade caused by buildings and trees was taken into account for the calculation of solar radiation. The sum of solar radiation of all cells (Solar_SUM) of a given radius is indicative of sun availability and thus indirectly of temperature. The standard deviation of solar radiation for all cells of a given radius indicates its variability for the focal radius (labeled Solar_STD).

Additionally, we obtained an index for woody plant cover (trees and bushes) based on the digital surface model. All cells higher than 1m that are not depicted as buildings in the building layer of the land cover layers of the topographic map 1:25’000 were classified as woody plants. The laser scanning method used in the creation of the Digital Surface Models underestimates the height of trees and bushes as the laser is not always reflected by the top foliage and is mostly reflected by lower levels. So, our measurement of woody plants is a minimum value.

As explained above, selection of location were effected along the minimum and maximum values of the three main gradients for each city were: ‘age of green area’ (Lugano: 1-106 years, Lucerne: 1-156, Zurich 1-156), ‘impervious area’ in the 50m radius (Lugano: 10.6-85.2%, Lucerne: 6.5-86.3%, Zurich: 2.5-91.8%; 100 % = 0.79ha), and ‘management intensity (Lugano: 1-20 cuts/vegetation period, Lucerne: 0-16, Zurich 1-13).

The results of the circular analysis are sometimes generalized as the influence of spatial scale, which is potentially misleading since the term space is used in multiple ways (Dungan et al. 2002). In this study, we measure habitat cover at different radii (extent) and reserve the term spatial variables to identify processes leading to spatial autocorrelation.

To allow for curvilinear effects of the explanatory variables, we incorporated linear and quadratic terms for all but the four measures for exposition. In total we had 16 predictor variables for the environmental data set ‘local variables’, ten for the data set ‘R50m’ (no agriculture in this radius) and twelve each for ‘R250m’ and ‘R1000m’.

4.3.5 Spatial predictors

Moran eigenvector maps (MEMs, Dray et al. 2006) were used to obtain spatial predictor variables that can be used in regression or ordination. MEMs represent the generalized form of the previously developed principal coordinates of neighbor matrices (PCNM, Borcard and Legendre 2002). Both methods use the eigenfunctions of the spatial configuration (= connectivity) matrices. The resulting variables (eigenvectors) are orthogonal to each other, so they are additive in scale-specific models (Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). MEM variables are more flexible to geographically irregular sampling schemes, as it was the case in our cities, and a wider array of connectivity matrices can be applied than in the classical PCNM approach. According to Dray et al. (2006), we proceeded as follows:

1) We obtained a Connectivity Matrix (**B** = $[b_{ij}]$) based on coordinates of sampling locations. We used Delaunay Triangulation (Legendre and Legendre 1998) to define neighboring locations. Thereby we excluded connections that cross lakes, as we assume that spatial processes crossing the open water are insignificant in our context.
2) We then computed a Euclidean distance matrix (**D** = $[d_{ij}]$) between neighboring locations and derived a weighting matrix **A** where $[a_{ij}] = 1/[d_{ij}]$.
3) The Connectivity Matrix **B** is weighted according to this distance, meaning that locations that are closer together are given greater weight (1/d) in the analysis. The final, spatial weighting matrix **W** results from the Hadamard (i.e., term-by-term) product of **B** and **A**.
4) Moran's eigenvectors and eigenvalues are calculated on the spatial weighting matrix **W**. The resulting variables are continuous.
5) The eigenvectors with positive eigenvalues, representing positive spatial autocorrelation, were included in data (see below) as spatial predictor (MEM) variables.

The MEM variables associated with small eigenvalues consist of fine waves with high frequency patterns and represent local structures, while those associated with large eigenvalues exhibit broad-scale frequency and represent scales on the maximum distances between sampling locations for each city (Lugano = 3.5 km , Lucerne = 4.3 km, Zurich = 6.2 km; Borcard and Legendre 2002, Dray et al. 2006). MEM eigenfunctions were created using the R-package 'spacemakeR' (Dray 2008).

4.3.6 Data analysis

Fig. 1 gives an overview of the data sets used and of the different steps of analysis to answer questions A-C. Unless otherwise stated, we used the R-language v2.6.0 (R Development Core Team 2007) for all statistical analysis. We Hellinger-transformed all community data (species per sampling location matrices) to make them appropriate for linear analyses (Legendre and Gallagher 2001). We tested the general null hypothesis that species community was not related to environmental or spatial variables.

Question A: For each of the three cities separately, we analyzed the community compositions of the focal taxa (birds, bees, spiders) with Redundancy analysis (RDA) with four environmental data sets measured at the four different radii. For each of the four environmental variable sets, we ran a forward selection with the R package packfor (Dray et al. 2007) to identify the significant variables ($p < 0.05$ after 9999 random permutations). We minimized the problems of the classical forward selection by applying the double-step procedure proposed by Blanchet et al. (2008). (1) Inflated Type I error was avoided by forward selecting only models for which a global test with all explanatory variables was significant. (2) To avoid overestimation of the amount of variance explained, another stopping criterion (next to the classical α rejection level) was introduced in that the adjusted coefficient of multiple determination (R^2_{adj}) of the model could not exceed the R^2_{adj} obtained when using all explanatory variables. Only the variables that fulfilled both stopping criteria were used in subsequent analyses.

Question B: We applied variation partitioning to determine the unique and joint fractions of variation explained by the four environmental data sets. Variation partitioning is implemented in the 'vegan' package (Oksanen et al. 2008). We report the variation explained in each RDA model as the adjusted R^2 (R^2_{adj}) which takes the number of predictor variables and sample size into account to prevent the inflation of R^2 values (Peres-Neto et al. 2006). When a negative R^2_{adj} was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006) meaning that not all fractions of one variation partitioning always add up to a perfect 100%. The first two canonical axes of the RDA analyses are illustrated with biplots using Canoco 4.5 (Ter Braak and Smilauer 2002).

Question C: We used the environmental variables and the spatial variables in another variation partitioning to assess the unique and joint fractions of variation explained by these matrices. For the environmental information we used the previously forward selected variables. For the spatial information we forward selected the MEM variables with the R-library 'packfor', but in this case we chose a relaxed, single-criterion forward selection (α = 0.05, 9999 permutations). We did so for exploratory purposes, to avoid a too high type II error level. We repeated this procedure for each city individually so that a different number of MEM variables were selected (Lugano = 9, Lucerne = 10, Zurich = 9). The species matrices (response variables) were checked for linear trends using RDA (explanatory variables: coordinates of sampling locations). Significant linear trends were removed by multiple regressions. The original Hellinger transformed species data or the detrended residuals were then used as response variables in the partial RDAs of the variation partitioning.

4.4 Results

Overall, we analyzed 21'048 spiders from 163 species, 6'194 bees from 139 species and 4'120 birds from 63 species. Species numbers per city, as the relevant summary for the statistical analysis, were in a similar order of magnitude for all groups and cities (Table 2). Detailed information on species' identities, steadiness and abundances are given in Supplementary material.

Forward selection identified the environmental variables that significantly explain variation in community composition of the three focal taxonomic groups (Table 3). For spider communities, six out of the eight selected variables stem from the local data set, while the remaining two were identified in the next smallest spatial extent, R50m, of Zurich. Together, environmental variables explained around 10% in all three cities (Zurich 12.1%, Lucerne 9.4%, Lugano 10.8%). No environmental variables measured on R250m and R1000m were selected in any of the three cities. Five of the selected variables can be circumscribed as temperature-relevant with two variables (Sun exposure^2, Solar_SUM R50m) directly measuring sun intensity and exposition and slope (Northness hillside (selected in two cities), Slope^2) controlling exposure to the sun. Management intensity (selected in two cities) indicates the susceptibility of spider communities to increased lawn/ meadow cuttings. The only habitat variable selected (Roads^2) points to the influence of an intermediate level of sealed area.

In all three cities bee communities were explained by single variables only and with very low fractions of explained variance (2-3% per variable). Together, environmental variables explained <6% in all three cities (Zurich 4.2%, Lucerne 4.0%, Lugano 5.9%) and no ecologically interpretable patterns could be identified.

Bird community compositions were explained by environmental variables in all four data sets. Together, environmental variables explained 15%-29% in the three cities (Zurich 16.0%, Lucerne 15.2%, Lugano 28.7%).One to three variables per city were derived from the R50m data set which explained 8-14% of the variation. Two variables per city were derived from the R250m data set, which explained 11-12%. From the R1000m data set, one variable each was chosen for Zurich and Lucerne (explaining 5% and 3%, respectively) while in Lugano four significant variables explained 17% of the variation. Between zero and two variables were selected from the local data set explaining 0-6% per city. The fraction of woody plants (i.e. trees and bushes as a linear or quadratic term; selected eight times), as well as the quantity and heterogeneity of solar radiation (linear or quadratic; selected seven times) measured on R50m, R250m and R1000m best explained bird communities. Other habitat cover variables were selected only four times.

Biplot illustrations for spiders and birds showing the first two canonical axes of the RDA analysis with the selected environmental variables and species are found in Supplementary material Fig. S2 and S3.

We standardized fractions of explained variation dividing the explained fraction by the total fraction which illustrates how much of the explained variation was shared among the different environmental variable sets (Table 4). Most of the standardized fractions for both spider communities (65-100%) and bird communities (49-72%) were explained by unique fractions (local, R50m, R250m, R1000m), i.e. the joint fractions were small. Nevertheless, in some cases the joint fractions of explained standardized variation took up significant portions For example, bird community in Zurich is explained to 34% by the joint fraction of the R50m and R250m data sets and to 20% by the joint fraction of the R50m, R250m and R1000m data sets.

Space-environment variation partitioning of the spider, bee and bird communities is displayed in Fig. 2. Even with an overall liberal, single stopping criterion in the forward selection of the MEM variables, almost no pure spatial structure could be detected in any taxa and city. Both spatial components, unique and joint, are usually small to negligible. In the case of spider communities, the variation explained by the spatial MEM variables was low (Zurich 3.3%, Lucerne 3.5%) or absent (Lugano). Spatial variables did not substantially increase the already minimal amount of explained variation for the bee community composition. Only in the case of the bird community in Lugano, the spatially structured environmental component reached a comparatively substantial value of 11.4%. In Zurich and Lucerne the MEM variables (unique and joint components) were low, explaining 2.5% and 3%, respectively.

4.5 Discussion

The comparison of the relative importance of environmental variables, reflecting niche processes, and of spatial variables, reflecting neutral processes, allows the identification of the major processes that shape communities. In all three study cities, we found a near absence of spatial organization in communities. Even with an overall liberal selection of the spatial variables, almost no purely spatial (PS) or spatially structured environmental (SSE) components could be detected.

This study shows that different taxonomic groups, i.e. spider and bird communities also respond to different sets of environmental variables at different spatial scales in urban environments. Spider communities react to very fine-scaled environmental changes of management and climate. Bee communities are a complex taxa without clear common patterns, contrary to bird communities which are strongly influenced by woody plants, i.e. trees and bushes, and solar radiation at several radii. First, we discuss patterns relating the taxa to significant variables of various nature and scale, thereafter we derive conclusions on how urban species communities are shaped.

4.5.1 Spiders

Forward selection of environmental variables at the four radii highlights the importance of fine-scaled factors for spiders. Only local and R50m variables explained the variation of spider communities. Studies in non-urban environments such as agriculture (Jeanneret et al. 2003), forest (Niemela et al. 1996) and the timberline (Muff et al. 2009) also identified the local scale as important for spiders.

The finding that micro-climatic variables describing exposition and sun intensity are key factors explaining spider communities in Swiss cities, conforms to previous studies in a US urban-desert landscape (Shochat et al. 2004), in fire-influenced forests (Moretti et al. 2002) and across an alpine timberline (Muff et al. 2009). In two cities (Zurich, Lucerne) we found management intensity to be a significant variable structuring spider communities. In grassland, the loss of structural complexity through increased management was also identified by Pozzi and Borcard (2001) as an important variable explaining spider communities.

Only few spider studies have incorporated spatial variables in their analyses. Most have included geographical coordinates (some including quadratic and cubic functions) and performed a trend surface analysis (Pozzi and Borcard 2001, Jeanneret et al. 2003, Jimenez-Valverde and Lobo 2007), while one study (Muff et al. 2009) considered PCNM variables. In strong contrast to our study in heavily disturbed urban environments, these studies, looking at semi-natural to natural habitats, found at least some significant autogenic spatial structure. Even though we included advanced MEM variables to model spatial variables, we found hardly any autogenic spatial structure.

In total, we explained 11-14% of total variation in spider communities. This rather low value compared to the studies mentioned above suggests that species compositions in urban spiders are far from characteristic species communities in given habitats but rather represent stochastic ad-hoc assemblages. Dispersal capacities, e.g. by ballooning and passive transportation by man, seem to allow spiders to colonize suitable fine-scaled habitats (regarding micro-climate, management) in a stochastic way in urban areas.

4.5.2 Bees

We found no common significant environmental factors that influence bee community composition in the three cities, with low proportions of total explained variance ($R^2_{adj} \approx 5\%$ in all cities). The few published studies of bees in urban environments have reported similar results. Cane et al. (2006) suggest that the ecological complexity of the community as a whole hides straightforward explanations. When comparing certain guilds, they found that cavity nesting species increased with urbanization due to increasing availability of firm features while ground nesting species decreased due to shrinking suitable habitat. Flying distances for bees have long been underestimated. In a genetic study of two bumble bee species in London (UK), Chapman et al. (2003) found little or no genetic differentiation at the landscape scale. Workers sampled on a small area of one hectare stem from a modeled average number of 96 (*Bombus terrestris*) and 66 colonies (*B. pascuorum*), respectively. These colonies are supposed to stem from great areas suggesting that workers traveled far to visit the site. Both species are also present in all three cities of the present study. Bee distribution depends on two main resources: suitable nesting substrate and nectar-offering plants. In urban areas, these resources are expected to be patchily distributed, possibly with considerable distances between them. Sampled bee species may just reflect that the sampling location was on the bee’s route to the foraging ground. In this case, the identification of significant variables is inhibited with our approach.

4.5.3 Birds

We found that environmental variables on all four radii were significant in explaining bird communities. Local variables explained little variation (0-6%), R50m variables with 8-14% and R250m with 11-12% explained considerable amounts while R1000m explained varying fractions (3%, 5%, 17%). These findings agree with those of Melles et al. (2003) who found that both local- and landscape-scale resources were important in determining the distribution of urban birds in British Columbia, Canada. Actually, studies that looked at a specific radius (house properties (Sattler and Tobler 2004), radius 25m (Palomino and Carrascal 2006), one ha (Goldstein et al. 1986), 1000m radius (Melles et al. 2003)) all found significant relationships for urban avian diversity on their respective scales. Also for forests, it was found that environmental variables at several spatial scales explain avian communities with small radii of app. 50m often contributing most to the explained variation (Cushman and McGarigal 2002, Yamaura et al. 2008). Melles et al. (2003) and Betts et al. (2006) suggested that the underlying mechanism for this pattern is that individual species show variable reactions at different spatial scales.

Woody plant as well as solar radiation variables, measured on all three radii (R50m, R250m and R1000m), were selected to explain avian communities. Woody plant variables reflect a diverse vertical habitat structure which is dominated by trees (Fontana et al. submitted). The importance of woody plants corroborates several previous studies which found that trees play an important role in explaining urban bird diversity (Goldstein et al. 1986, Palomino and Carrascal 2006, Sandstrom et al. 2006, Fontana et al. submitted). The influence of solar radiation at fine scales, reflecting microclimatic conditions, has rarely been analyzed for its effect on birds. However, the observed influence of solar radiation is not uniform. As an example, Fig. S3 C (Supplementary material) shows that the standard deviation of solar radiation on R50m and R250m points to the opposite direction of the sum of solar radiation on R250m and R1000m. Standard deviation of solar radiation reflects a structurally highly diversified habitat, which in turn causes high variability of solar radiation. Specific studies that control for these effects are needed to disentangle possible interactions of these properties at various spatial scales.

We identified a substantial SSE component (11.7%; Fig. 2) only in Lugano. The cause for this high fraction (in comparison with the values for the other taxa in this urban study) is uncertain. The reason that bird-relevant environmental variables are more spatially structured in Lugano than in other cities may be related to the small size of the city and its position in a hilly area. We found that the PS component was virtually absent in all three cities. Spatial variables explain bird communities in other habitats types. Yamaura et al. (2008) analyzed bird communities in forests with PCNM variables and attributed 9-19% to PS effects. Miller et al. (2003) included the y coordinate and a distance from water source as measures for spatial variables and explained 18.5% of the variation. This overview on spatial components explaining bird communities leads us to conclude that increased disturbance of the urban habitat by man may interfere with autogenic processes in bird communities and thus likely be the cause for the observed absence of PS effects. In original (forest) habitats the spatial structure seems to be an important factor progressively declining through agricultural-forest mosaics to urban areas.

4.5.4 Conclusions

Our empirical evidence showing the absence of pure spatial component suggests that neutral mechanisms, i.e. biotic processes such as dispersal and interspecific competition, play a subordinate to negligible role in structuring community composition in urban areas. We suggest that the manifold human activites in urban areas inhibit both the development and installation of spatially organized environmental variables and of biotic processes. We propose that the near absence of spatial structure is a characteristic typical to urban species assemblages. The urban environment constitutes a close-knit mosaic of habitats that are disturbed on a regular to frequent basis. Urban species are selected to cope with these heavy human influences. Some arthropods may even profit from regular but stochastic passive transportation by humans to colonize new and suitable habitat patches (Germann et al. 2008) and/or profit from other new opportunities arising in the city environment (e.g. abundant food, predator release). Species communities in urban areas are far from equilibrium and undergo constant change in adapting to the disturbances and changes that characterize their urban environments.

Acknowledgements

We thank the house owners that provided access to their properties and the authorities of Lucerne, Lugano and Zurich for their support of the project. We are grateful to the following people for support in field work or for determining the species: S. Fontana (birds); X. Heer (spiders); D. Kouakou, A. Müller, M. Hermann and F. Amiet (bees). P. Duelli helped in organizing the project, R. Home improved the English of earlier versions of the manuscript. T.S. thanks M. Lehmann for her manifold support.

GIS layers were obtained from the Swiss Federal Office of Topography (Vector25 © 2009 swisstopo, DV033594). This study forms part of the interdisciplinary project 'BiodiverCity' (www.biodivercity.ch) which aims at the identification, maintenance and enhancement of biodiversity and their acceptance in the urban development process. BiodiverCity was funded by the Swiss National Science Foundation as a project of NRP54 'Sustainable development of the built environment' (www.nrp54.ch).

4.6 References

Artuso, R., S. Bovet, and A. Streilein. 2003. Practical methods for the verification of countrywide terrain and surface models. International Archives for Photogrammetry, Remote Sensing and Spatial Information Sciences 34:6p. (on CD-ROM).

Bell, G. 2000. The distribution of abundance in neutral communities. American Naturalist 155:606-617.

Betts, M. G., G. J. Forbes, A. W. Diamond, and P. D. Taylor. 2006. Independent effects of fragmentation on forest songbirds: An organism-based approach. Ecological Applications 16:1076-1089.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000 Bird Census Techniques. Academic Press, London.

Blair, R. B. 1999. Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? Ecological Applications 9:164-170.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables. Ecology 89:2623-2632.

Böhning-Gaese, K. 1997. Determinants of avian species richness at different spatial scales. Journal of Biogeography 24:49-60.

Borcard, D., and P. Legendre. 1994. Environmental control and spatial structure in ecological communities: an example using Oribatid mites (Acari, Oribatei). Environmental and Ecological Statistics 1:37-61.

Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51-68.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826-1832.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73:1045-1055.

Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera : Apiformes) to urban habitat fragmentation. Ecological Applications 16:632-644.

Chapman, R. E., J. Wang, and A. F. G. Bourke. 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. Molecular Ecology 12:2801-2808.

Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology 17:637-646.

Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21:741-751.

Dray, S. 2008. SpacemakeR: Spatial modelling.

Dray, S., P. Legendre, and F. G. Blanchet. 2007. packfor: Forward Selection with permutation.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483-493.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agriculture Ecosystems & Environment 62:81-91.

Duelli, P., M. K. Obrist, and D. R. Schmatz. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture Ecosystems & Environment 74:33-64.

Dungan, J. L., J. N. Perry, M. R. T. Dale, P. Legendre, S. Citron-Pousty, M. J. Fortin, A. Jakomulska, M. Miriti, and M. S. Rosenberg. 2002. A balanced view of scale in spatial statistical analysis. Ecography 25:626-640.

Fontana, S., T. Sattler, F. Bontadina, and M. Moretti. submitted. How to manage the urban green to enhance bird species richness and diversity. Biological Conservation.

Fortin, D. and M. R. T. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press.

Germann, C., T. Sattler, M. K. Obrist, and M. Moretti. 2008. Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 81 141-154.

Goldstein, E. L., M. Gross, and R. M. Degraaf. 1986. Breeding Birds and Vegetation – a Quantitative Assessment. Urban Ecology 9:377-385.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson, G. E. 1957. Concluding remarks. Pages 415–427 in Harbor Symposium on Quantitative Biology, Population Studies: Animal Ecology and Demography, Cold Spring Harbour.

Jeanneret, P., B. Schupbach, L. Pfiffner, and T. Walter. 2003. Arthropod reaction to landscape and habitat features in agricultural landscapes. Landscape Ecology 18:253-263.

Jimenez-Valverde, A., and J. M. Lobo. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecological Entomology 32:113-122.

Johnston, C. A., D. M. Ghioca, M. Tulbure, B. L. Bedford, M. Bourdaghs, C. B. Frieswyk, L. Vaccaro, and J. B. Zedler. 2008. Partitioning vegetation response to anthropogenic stress to develop multi-taxa wetland indicators. Ecological Applications 18:983-1001.

Jombart, T., S. Dray, and A. B. Dufour. 2009. Finding essential scales of spatial variation in ecological data: a multivariate approach. Ecography 32:161-168.

Jones, M. M., H. Tuomisto, D. Borcard, P. Legendre, D. B. Clark, and P. C. Olivas. 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155:593-604.

Kivinen, S., M. Luoto, M. Kuussaari, and K. M. Saarinen. 2007. Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. Agriculture Ecosystems & Environment 122:453-460.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution 14:22-26.

Legendre, P. 1993. Spatial Autocorrelation – Trouble or New Paradigm. Ecology 74:1659-1673.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs 75:435-450.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280.

Legendre, P., and L. Legendre. 1998. Numerical ecology. 2nd edition. Elsevier Science PV, Amsterdam.

Legendre, P., X. C. Mi, H. B. Ren, K. P. Ma, M. J. Yu, I. F. Sun, and F. L. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Luoto, M., R. Virkkala, and R. K. Heikkinen. 2007. The role of land cover in bioclimatic models depends on spatial resolution. Global Ecology and Biogeography 16:34-42.

Melles, S., S. Glenn, and K. Martin. 2003. Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. Conservation Ecology 7.

Miller, J. R., J. A. Wiens, N. T. Hobbs, and D. M. Theobald. 2003. Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecological Applications 13:1041-1059.

Moretti, M., M. Conedera, P. Duelli, and P. J. Edwards. 2002. The effects of wildfire on ground-active spiders in deciduous forests on the Swiss southern slope of the Alps. Journal of Applied Ecology 39:321-336.

Muff, P., C. Kropf, H. Frick, W. Nentwig, and M. H. Schmidt-Entling. 2009. Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline. Insect Conservation and Diversity 2:36-44.

Niemela, J., Y. Haila, and P. Punttila. 1996. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19:352-368.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, M. H. H. Stevens, and H. H. Wagner. 2008. vegan: Community Ecology Package.

Palomino, D., and L. M. Carrascal. 2006. Urban influence on birds at a regional scale: A case study with the avifauna of northern Madrid province. Landscape and Urban Planning 77:276-290.

Pellet, J., A. Guisan, and N. Perrin. 2004. A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conservation Biology 18:1599-1606.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87:2614-2625.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.

Pozzi, S., and D. Borcard. 2001. Effects of dry grassland management on spider (Arachnida : Araneae) communities on the Swiss occidental plateau. Ecoscience 8:32-44.

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. Sankhyaa, Series A 26:329-358.

Rebele, F. 1994. Urban Ecology and Special Features of Urban Ecosystems. Global Ecology and Biogeography Letters 4:173-187.

Sandstrom, U. G., P. Angelstam, and G. Mikusinski. 2006. Ecological diversity of birds in relation to the structure of urban green space. Landscape and Urban Planning 77:39-53.

Sattler, T., P. Duelli, M. K. Obrist, R. Arlettaz, and M. Moretti. submitted. Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecology.

Sattler, T., and M. Tobler. 2004. Development of breeding populations of birds in two residential areas in Solothurn and their dependence on habitat structure (in German with English summary). Der Ornithologische Beobachter 101:177-192.

Shochat, E., W. L. Stefanov, M. E. A. Whitehouse, and S. H. Faeth. 2004. Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. Ecological Applications 14:268-280.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421-1432.

Sukopp, H., and Wittig, R. 1998. Stadtökologie. 2nd edition. Fischer, Stuttgart: 474 p.

Ter Braak, C. J. F., and P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user’s guide: software for canonical community ordination (ver. 4.5). Microcomputer Power, New York.

Wagner, H. H. 2003. Spatial covariance in plant communities: Integrating ordination, geostatistics, and variance testing. Ecology 84:1045-1057.

Yamaura, Y., K. Katoh, and T. Takahashi. 2008. Effects of stand, landscape, and spatial variables on bird communities in larch plantations and deciduous forests in central Japan. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 38:1223-1243.

4.7 Tables and figures

Table 1: Environmental variables used in the analysis. Variables are listed according to 'local', and the three radii 'R50m', 'R250m', 'R1000m' (for further details see Methods).

Name	Explanation	Unit
1. Local variables		
Elevation	Meter above sea level	m
Slope		%
Eastness trap	Exposition of trap location with respect to East	Gradient: -1 to 1
Northness trap	Exposition of trap location with respect to North	Gradient: -1 to 1
Eastness hillside	Exposition of hillside with respect to East	Gradient: -1 to 1
Northness hillside	Exposition of hillside with respect to North	Gradient: -1 to 1
Age	Time since last structural modification of green area	Years
Management intensity	Cutting frequency of meadow/lawn during the vegetation period	number of cuts in 26 weeks
Soil density[1]	Soil density Index	cm
Sun exposure	Time of sun exposure in July	Hours
2.-4. Land cover map and solar radiation measured in radius 50m, 250m, 1000m		
Agriculture[2]	Agricultural area (only radius 250m and 1000m)	m^2
Roads[2]	Area sealed by roads (width according to road class)	m^2
Urban Green[2]	Area of Urban Green	m^2
Woody plants[3]	Area of trees and bushes	m^2
Solar_STD[3]	Standard Deviation of Solar Radiation	Watt hours/m^2
Solar_SUM[3]	Sum of Solar Radiation	Watt hours/m^2

[1] Measured with a self-made iron stick and a constant weight

[2] Obtained from theme specific layer of the topographic map 1:25000 of Switzerland

[3] Obtained from Digital Surface Model (Artuso et al. 2003)

Table 2: Summary results of the three taxa groups spiders (Araneae), bees (Apidae) and birds (Aves) analyzed per city.

		Zurich	**Luzern**	**Lugano**	**Total**
Araneae	N individuals	6039	7707	7302	21048
	N species	94	89	82	163
	Species mean ± SD (min - max) / sampling location	16.8 ± 4.7 (10 – 28)	16.3 ± 4.5 (9 – 26)	14.0 ± 4.5 (5 – 24)	
Apidae	N individuals	2085	1594	2515	6194
	N species	80	73	102	139
	Species mean ± SD (min - max) / sampling location	15.7 ± 6.0 (7 – 27)	14.5 ± 5.8 (5 – 31)	18.8 ± 6.8 (8 – 35)	
Aves	N individuals	1321	1374	1425	4120
	N species	42	51	40	63
	Species mean ± SD (min - max) / sampling location	15.0 ± 3.7 (10 – 26)	17.4 ± 4.4 (10 – 26)	16.1 ± 3.1 (8 – 22)	

Table 3: Selected environmental variables explaining community composition of the three taxa groups spiders, bees and birds for each of the four data sets (local, R50m, R250m, R1000m), separated by taxa group and city; 'ns' = no significant variables identified.

		local	**R50m**	**R250m**	**R1000m**
Spiders	Zurich	Management intensity (5.3%) Northness hillside (2.5%)	Roads^2 (3.7%) Solar_SUM (4.7%)	ns	ns
	Lucerne	Management intensity (7.2%) Northness hillside (2.3%)	ns	ns	ns
	Lugano	Sun exposure^2 (5.5%) Slope^2 (5.3%)	ns	ns	ns
Bees	Zurich	ns	ns	ns	Roads^2 (2.9%)
	Lucerne	ns	Urban Green (3.1%)	Roads^2 (3.2%)	Agriculture (2.7%)
	Lugano	Age (2.5%)	ns	Solar_SUM (2.3%)	ns
Birds	Zurich	ns	Woody plants^2 (6.2%) Solar_SUM (3.9%) Urban Green^2 (2.4%)	Woody plants^2 (6.4%) Agriculture (4.2%)	Solar_STD^2 (4.6%)
	Lucerne	Elevation (3.6%)	Woody plants (7.8%)	Solar_SUM (8.8%) Woody plants (2.1%)	Woody plants (3.4%)
	Lugano	Elevation (3.8%) Slope^2 (2.2%)	Woody plants (7.3%) Solar_STD^2 (4.5%) Solar_STD (2.3%)	Woody plants (8.0%) Solar_SUM (4.0%)	Solar_SUM^2 (3.8%) Woody plants (7.1%) Agriculture (2.7%) Urban Green^2 (2.9%)

Table 4: Standardised fraction of explained variation (100% = total explained variation of selected variables) for each individual data set (local, R50m, R250m, R1000m) and for categories of shared explained variation between the four environmental data sets, separated by taxa group and city. A reading example for categories of joint explained variation: the column ‘local/R50m indicates that this fraction of explained variation is equally shared by the data sets ‘local’ and ‘R50m’. ‘ns’ = no significant variables identified; ‘-‘ = shared component not available (1 or more data sets had no significant variables); cells left blank indicate negative values (omitted because not interpretable, see methods – in these cases fractions of explained variance sum to >100%.

Data set	local	R50m	R250m	R1000m	local/R50m	R50m/R250m	R250m/R1000m	local/R1000m	R50m/R1000m	local/R250m	local/R50m/R1000m	local/R50m/R250m	R50m/R250m/R1000m	local/R250m/R1000m	local/R50m/R250m/R1000m
Araneae															
Zurich	30.6%	34.3%	ns	ns	35.1%	-	-	-	-	-	-	-	-	-	-
Lucerne	100.0%	ns	ns	ns	-	-	-	-	-	-	-	-	-	-	-
Lugano	100.0%	ns	ns	ns	-	-	-	-	-	-	-	-	-	-	-
Apidae															
Zurich	ns	ns	30.9%	7.9%	-	-	61.2%	-	-	-	-	-	-	-	-
Lucerne	ns			44.2%	-	74.2%		-	0.4%	-	-	-	26.5%	-	-
Lugano	33.6%	ns	8.9%	ns	-	-	-	-	-	57.5%	-	-	-	-	-
Aves															
Zurich	ns	26.0%	12.8%	9.9%	-	33.5%		-		-	-	-	19.8%	-	-
Lucerne		27.8%	17.3%	10.4%	0.2%	8.7%	12.1%	0.4%		15.6%		18.0%	0.0%		0.3%
Lugano	6.1%	22.4%	14.3%	28.7%	0.8%						4.8%	1.7%	15.5%	7.4%	5.5%

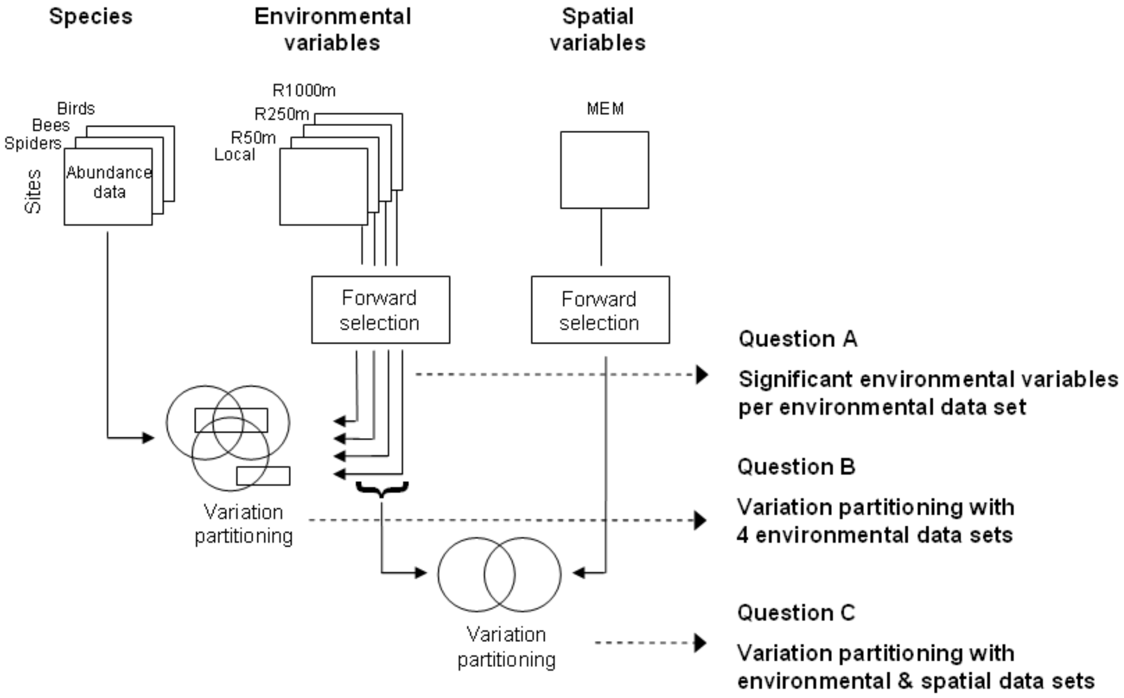

Fig. 1: Diagram of the different data sets used and the analytical steps performed with respect to the 3 study questions. These steps were repeated for every city individually.

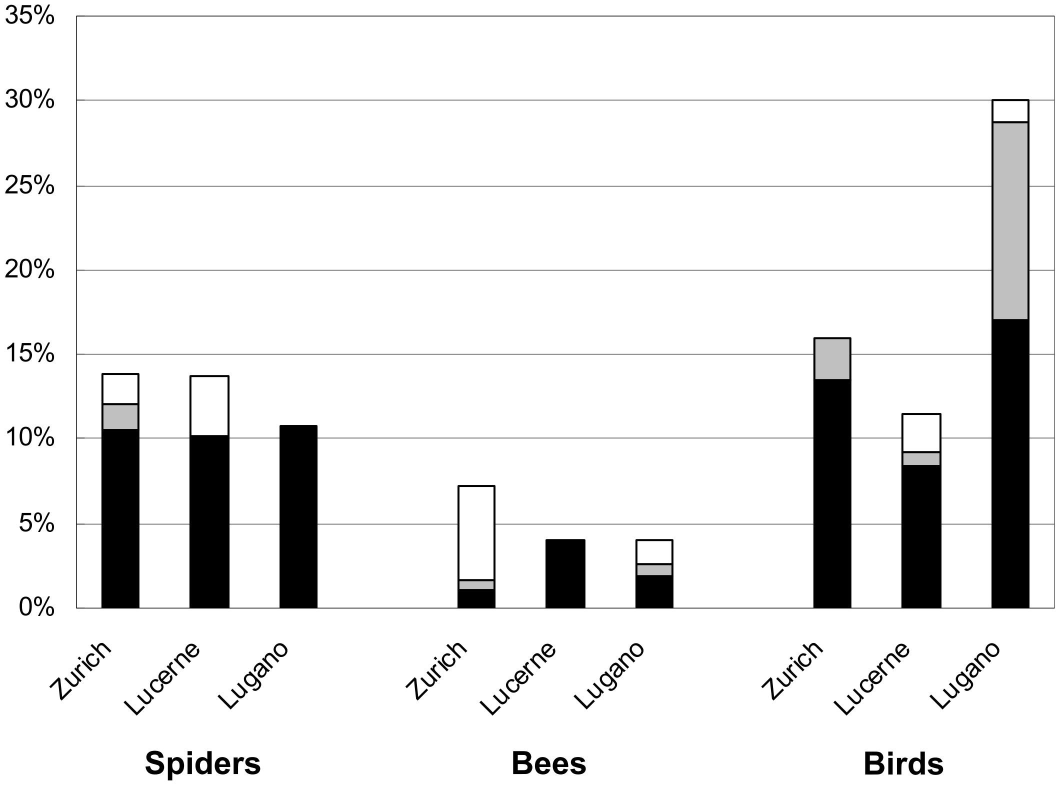

Fig. 2: Results of variation partitioning (Borcard et al. 1992) to separate the purely environmental, the spatially structured environmental, and the purely spatial component of variance explaining community composition of the three taxa groups spiders (Araneae), bees (Apidae) and birds (Aves). The selected variables of the four environmental data sets (local, R50m, R250m, R1000m) formed the environmental information, the selected MEM variables were used for the spatial information. See methods for details. Black = purely environmental; Gray = spatially structured environmental; White = purely spatial.

4.8 Supplementary material

Table S1 A: Spider species (Araneae) according to the three study cities. In total 21’048 spiders from 163 species were collected in the 96 locations (32 per city; for details per city see Table 2). Steadiness expresses the number of sampling points with the presence of the species. Dominance indicates the fraction (%) of individuals of a single species on the total individual number of spiders. Dominance = % individuals; Steadiness = % locations with presence.

All figures in %		**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Abbreviations[1]**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**
Achaearanea riparia	*Achrip*	0.017	3.1				
Achaearanea simulans	*Achsim*	0.017	3.1	0.039	9.4		
Achaearanea tepidariorum	*Achtep*	0.017	3.1				
Agelena gracilens	*Agegra*	0.033	6.3				
Agelena labyrinthica	*Agelab*			0.039	6.3		
Alopecosa cuneata	*Alocun*	0.017	3.1				
Alopecosa pulverulenta	*Alopul*	1.739	34.4	0.558	3.1	0.603	21.9
Alopecosa trabalis	*Alotra*					0.014	3.1
Anelosimus vittatus	*Anevit*			0.013	3.1		
Araeoncus humilis	*Arahum*	0.745	50.0	0.208	18.8	0.014	3.1
Araneus triguttatus	*Aratri*	0.017	3.1	0.013	3.1		
Araniella cucurbitina	*Aracuc*	0.066	12.5	0.130	25.0	0.055	12.5
Arctosa leopardus	*Arcleo*	0.066	6.3	10.056	78.1	2.492	28.1
Arctosa lutetiana	*Arclut*			0.026	3.1	0.110	15.6
Arctosa personata	*Arcper*					0.247	12.5
Atypus affinis	*Atyaff*	0.017	3.1	0.013	3.1	0.055	12.5
Aulonia albimana	*Aulalb*	0.066	6.3				
Bathyphantes gracilis	*Batgra*	0.017	3.1	0.013	3.1	0.055	9.4
Ceratinella brevis	*Cerbre*					0.219	3.1
Cheiracanthium mildei	*Chemil*	0.099	15.6	0.013	3.1	0.027	6.3
Clubiona brevipes	*Clubre*	0.066	12.5	0.013	3.1		
Clubiona comta	*Clucom*	0.017	3.1				
Clubiona genevensis	*Clugen*					0.014	3.1
Clubiona pallidula	*Clupal*			0.013	3.1		
Clubiona terrestris	*Cluter*	0.033	6.3				
Cnephalocotes obscurus	*Cneobs*	0.265	18.8	0.921	43.8	0.110	12.5
Cnephalocotes sanguinolentus	*Cnesan*	0.050	9.4			0.356	3.1
Collinsia inerrans	*Coline*	0.033	6.3				
Diaea dorsata	*Diador*			0.013	3.1		
Dictyna arundinacea	*Dicaru*	0.033	6.3				
Dictyna pusilla	*Dicpus*	0.017	3.1				
Dicymbium nigrum	*Dicnig*	0.480	34.4	0.221	25.0	0.014	3.1

Dicymbium tibiale	*Dictib*	0.033	3.1				
Diplocephalus cristatus	*Dipcri*	0.050	3.1	0.234	9.4		
Diplocephalus latifrons	*Diplat*	0.017	3.1	0.208	3.1	0.425	12.5
Diplostyla concolor	*Dipcon*	0.116	15.6	0.311	15.6		
Dipoena erythropus	*Dipery*					0.027	6.3
Dipoena melanogaster	*Dipmel*	0.033	6.3	0.013	3.1	0.027	6.3
Dipoena prona	*Dippro*					0.014	3.1
Drassyllus praeficus	*Drapra*					0.014	3.1
Drassyllus pumilus	*Drapum*					0.014	3.1
Drassyllus pusillus	*Drapus*	0.232	18.8			0.096	12.5
Drassyllus villicus	*Dravil*					0.027	3.1
Dysdera crocata	*Dyscro*					0.014	3.1
Dysdera erythrina	*Dysery*	0.050	3.1				
Enoplognatha latimana	*Enolat*	0.017	3.1	0.013	3.1		
Enoplognatha thoracica	*Enotho*	0.911	6.3	0.558	40.6	0.027	6.3
Entelecara acuminata	*Entacu*			0.026	6.3		
Entelecara congenera	*Entcon*			0.013	3.1		
Eperigone trilobata	*Epetri*	8.727	100.0	4.165	96.9	3.191	75.0
Episinus angulatus	*Epiang*			0.026	3.1		
Episinus truncatus	*Epitru*					0.014	3.1
Erigone atra	*Eriatr*	1.722	50.0	1.920	78.1		
Erigone autumnalis	*Eriaut*					10.942	9.4
Erigone dentipalpis	*Eriden*	34.112	9.4	20.293	9.4	16.872	87.5
Erigonella hiemalis	*Erihie*			0.026	3.1		
Ero aphana	*Eroaph*	0.033	6.3	0.026	6.3		
Euophrys erratica	*Euoerr*					0.014	3.1
Euophrys frontalis	*Euofro*	0.149	9.4			0.041	6.3
Euophrys lanigera	*Euolan*					0.014	3.1
Gongylidiellum latebricola	*Gonlat*			0.013	3.1		
Hahnia helveola	*Hahhel*	0.017	3.1				
Hahnia nava	*Hahnav*	0.348	18.8				
Heliophanus auratus	*Helaur*	0.033	6.3	0.013	3.1		
Heliophanus cupreus	*Helcup*					0.082	3.1
Heliophanus flavipes	*Helfla*	0.182	9.4	0.195	18.8	0.205	15.6
Heliophanus tribulosus	*Heltri*					0.014	3.1
Histopona torpida	*Histor*			0.052	9.4		
Icius subinermis	*Icisub*	0.017	3.1				
Keijia tincta	*Keitin*	0.033	6.3	0.013	3.1		
Larinioides patagiatus	*Larpat*	0.017	3.1				
Linyphia hortensis	*Linhor*			0.013	3.1		
Linyphia triangularis	*Lintri*			0.013	3.1		
Macaroeris nidicolens	*Macnid*	0.033	6.3			0.014	3.1
Maso sundevalli	*Massun*	0.017	3.1				
Meioneta fuscipalpa	*Meifus*					0.014	3.1
Meioneta mollis	*Meimol*					0.520	50.0
Meioneta rurestris	*Meirur*	4.537	9.4	2.219	78.1	10.189	100.0
Meioneta saxatilis	*Meisax*	0.017	3.1			0.041	9.4
Micaria pulicaria	*Micpul*	0.033	6.3	0.156	15.6	0.164	15.6
Micrargus herbigradus	*Micher*	0.017	3.1				
Micrargus subaequalis	*Micsub*	0.695	3.1	0.169	6.3		

Microlinyphia pusilla	*Micpus*	0.017	3.1			0.014	3.1
Misumena vatia	*Misvat*	0.017	3.1	0.013	3.1		
Monocephalus fuscipes	*Monfus*	0.017	3.1				
Myrmarachne formicaria	*Myrfor*			0.052	6.3	0.014	3.1
Neottiura bimaculata	*Neobim*	0.033	6.3	0.013	3.1		
Neriene clathrata	*Nercla*			0.026	3.1		
Nigma flavescens	*Nigfla*	0.017	3.1				
Oecobius maculatus	*Oecmac*					0.041	9.4
Oedothorax apicatus	*Oedapi*	0.679	12.5	0.039	9.4	0.082	9.4
Oedothorax fuscus	*Oedfus*	2.037	3.1	17.555	6.3	14.256	6.3
Ozyptila praticola	*Ozypra*	0.050	6.3				
Ozyptila sanctuaria	*Ozysan*					0.110	18.8
Ozyptila simplex	*Ozysim*					0.137	9.4
Ozyptila trux	*Ozytru*					0.014	3.1
Pachygnatha clercki	*Paccle*	0.033	3.1	0.026	6.3		
Pachygnatha degeeri	*Pacdeg*	18.480	81.3	17.322	90.6	4.232	59.4
Pachygnatha sp.	*Pacsp.*			1.518	3.1		
Pardosa agrestis	*Paragr*	0.828	12.5	0.013	3.1		
Pardosa amentata	*Parame*	0.348	15.6	2.855	37.5		
Pardosa hortensis	*Parhor*	1.888	53.1	0.804	21.9		
Pardosa palustris	*Parpal*	4.603	40.6	0.804	34.4		
Pardosa proxima	*Parpro*			0.039	3.1	16.954	71.9
Pardosa pullata	*Parpul*	0.629	6.3	0.519	6.3		
Pardosa saltans	*Parsal*	0.017	3.1	0.026	3.1		
Pelecopsis parallela	*Pelpar*			0.026	3.1		
Philodromus albidus	*Phialb*			0.065	9.4		
Philodromus aureolus	*Phiaur*	0.033	6.3	0.130	12.5		
Philodromus buxi	*Phibux*					0.014	3.1
Philodromus collinus	*Phicol*	0.033	3.1	0.065	12.5		
Philodromus praedatus	*Phipra*			0.013	3.1		
Philodromus rufus	*Phiruf*	0.017	3.1			0.027	6.3
Phlegra fasciata	*Phlfas*	0.149	12.5	0.039	3.1		
Phrurolithus festivus	*Phrfes*	1.904	6.3	0.311	3.1	0.055	12.5
Pirata hygrophilus	*Pirhyg*			0.026	3.1		
Pirata latitans	*Pirlat*	1.275	3.1	6.462	56.3		
Pisaura mirabilis	*Pismir*	0.066	6.3	0.013	3.1		
Pocadicnemis juncea	*Pocjun*			0.039	6.3	0.014	3.1
Porrhomma microphthalmum	*Pormic*			0.026	6.3		
Porrhomma pygmaeum	*Porpyg*	0.017	3.1				
Prinerigone sp.	*Prisp.*					0.520	28.1
Pseudomaro aenigmaticus	*Pseaen*			0.013	3.1		
Saaristoa abnormis	*Saaabn*			0.013	3.1		
Saloca diceros	*Saldic*			0.026	6.3		
Salticus cingulatus	*Salcin*					0.014	3.1
Salticus scenicus	*Salsce*	0.017	3.1			0.014	3.1
Scytodes thoracica	*Scytho*	0.017	3.1				
Sitticus distinguendus	*Sitdis*					0.041	3.1
Steatoda bipunctata	*Stebip*			0.013	3.1		
Steatoda italica	*Steita*					0.630	37.5

Steatoda phalerata	*Stepha*					0.247	21.9
Synema globosum	*Synglo*					0.041	9.4
Talavera aequipes	*Talaeq*					0.014	3.1
Tenuiphantes flavipes	*Tenfla*					0.027	6.3
Tenuiphantes tenuis	*Tenten*	0.331	21.9	0.091	21.9	0.123	12.5
Tetragnatha montana	*Tetmon*	0.050	9.4	0.039	9.4		
Tetragnatha nigrita	*Tetnig*			0.013	3.1		
Tetragnatha obtusa	*Tetobt*	0.017	3.1	0.026	6.3		
Tetragnatha pinicola	*Tetpin*	0.083	3.1				
Theridion impressum	*Theimp*	0.099	15.6	0.013	3.1	0.014	3.1
Theridion nigrovariegatum	*Thenig*					0.096	15.6
Theridion pallens	*Thepal*	0.017	3.1	0.039	9.4		
Theridion pinastri	*Thepin*	0.116	18.8	0.597	21.9		
Theridion varians	*Thevar*	0.182	15.6	0.169	3.1	0.055	12.5
Tiso vagans	*Tisvag*	3.229	71.9	4.386	84.4	0.753	15.6
Trichopterna cito	*Tricit*					1.438	43.8
Trochosa ruricola	*Trorur*	3.444	71.9	1.336	56.3	1.411	65.6
Trochosa terricola	*Troter*	0.464	21.9	0.454	40.6		
Walckenaeria antica	*Walant*	0.331	28.1	0.208	25.0		
Walckenaeria vigilax	*Walvig*	0.116	3.1				
Xerolycosa miniata	*Xermin*	0.066	6.3			9.806	65.6
Xerolycosa nemoralis	*Xernem*					0.123	3.1
Xysticus cristatus	*Xyscri*	0.977	50.0	0.285	34.4		
Xysticus erraticus	*Xyserr*			0.013	3.1	0.301	15.6
Xysticus kochi	*Xyskoc*	0.298	25.0	0.156	15.6	0.452	28.1
Xysticus lanio	*Xyslan*					0.014	3.1
Zelotes exiguus	*Zelexi*					0.274	34.4
Zelotes hermani	*Zelher*					0.014	3.1
Zelotes petrensis	*Zelpet*					0.027	3.1
Zelotes tenuis	*Zelten*					0.014	3.1
Zodarion italicum	*Zodita*	0.845	6.3	0.285	28.1	0.110	12.5
Zodarion rubidum	*Zodrub*					0.068	15.6

[1] see Fig. S2 A, B, C

Table S1 B: Bee species (Apidae) according to the three study cities. In total 6'194 bees from 139 species were collected in the 96 locations (32 per city; for details per city see Table 2). Steadiness expresses the number of sampling points with the presence of the species. Dominance indicates the fraction (%) of individuals of a single species on the total individual number of bees.

All figures in %	**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**	**Dominance**	**Steadiness**
Andrena bicolor	0.19	12.50	0.25	12.50		
Andrena bimaculata					0.83	28.13
Andrena bucephala	0.05	3.13				
Andrena carantonica	0.05	3.13	0.13	6.25	0.16	12.50
Andrena chrysosceles	0.10	6.25			0.04	3.13
Andrena dorsata			0.06	3.13	0.40	25.00
Andrena flavipes	0.19	9.38	0.13	3.13	0.08	6.25
Andrena florea					0.04	3.13
Andrena fulvago	0.19	12.50	0.50	18.75	0.08	3.13
Andrena gelriae	0.05	3.13	0.13	3.13	0.32	12.50
Andrena gravida	0.05	3.13				
Andrena haemorrhoa			0.06	3.13		
Andrena hattorfiana					0.12	6.25
Andrena humilis			0.06	3.13		
Andrena minutula	0.29	15.63	0.31	12.50	0.24	15.63
Andrena minutuloides			0.06	3.13	0.04	3.13
Andrena nitidiuscula	0.05	3.13				
Andrena ovatula	0.34	15.63	0.50	18.75	0.99	31.25
Andrena pandellei	0.05	3.13				
Andrena rosae					0.36	15.63
Andrena tibialis					0.12	6.25
Andrena trimmerana					0.16	6.25
Andrena wilkella					0.04	3.13
Anthidium florentinum					0.04	3.13
Anthidium manicatum	0.43	28.13	0.56	21.88	0.28	21.88
Anthidium oblongatum			0.13	6.25	0.04	3.13
Anthidium scapulare					0.08	6.25
Anthidium septemspinosum					0.04	3.13
Anthidium strigatum					0.04	3.13
Bombus hortorum	0.86	34.38	1.88	50.00	0.44	28.13
Bombus humilis	0.38	21.88	0.38	9.38	0.08	6.25
Bombus hypnorum	0.96	34.38	0.38	12.50	0.12	9.38
Bombus lapidarius	7.24	87.50	3.01	46.88	2.39	75.00
Bombus lucorum	0.62	25.00	0.69	31.25	0.32	18.75

Bombus pascuorum	2.49	65.63	4.08	78.13	3.62	81.25
Bombus pratorum	0.34	15.63	0.63	25.00		
Bombus ruderarius	0.14	9.38				
Bombus terrestris	9.45	87.50	13.43	96.88	5.84	100.00
Bombus veteranus	0.05	3.13				
Ceratina cyanea					0.04	3.13
Chelostoma campanularum	0.19	3.13	0.06	3.13	0.12	9.38
Chelostoma distinctum	0.05	3.13	0.63	15.63	0.16	6.25
Chelostoma rapunculi	1.58	56.25	3.32	59.38	0.08	6.25
Coelioxys echinata					0.04	3.13
Coelioxys elongata					0.08	6.25
Colletes daviesanus			0.25	9.38		
Colletes similis	0.10	6.25	0.06	3.13		
Dasypoda hirtipes					0.04	3.13
Eucera longicornis			0.06	3.13		
Eucera nigrescens	0.10	6.25	0.06	3.13	0.04	3.13
Halictus confusus	0.24	12.50				
Halictus langobardicus	0.05	3.13			0.04	3.13
Halictus maculatus					0.32	18.75
Halictus rubicundus					0.80	40.63
Halictus scabiosae	0.62	12.50			0.04	3.13
Halictus sexcinctus					0.36	15.63
Halictus simplex	0.29	6.25			1.31	46.88
Halictus subauratus			0.06	3.13	2.74	71.88
Halictus tumulorum	2.35	65.63	1.25	37.50	0.12	9.38
Heriades crenulatus	0.10	6.25	0.31	15.63	0.48	6.25
Heriades truncorum	1.73	46.88	0.88	31.25	0.44	15.63
Hylaeus angustatus			0.13	3.13	0.04	3.13
Hylaeus annularis	0.05	3.13				
Hylaeus brevicornis			0.13	6.25		
Hylaeus communis	0.86	31.25	1.32	50.00	0.60	34.38
Hylaeus confusus	0.77	34.38	0.88	34.38	0.28	15.63
Hylaeus difformis	0.10	6.25			0.04	3.13
Hylaeus gredleri	0.19	12.50	0.13	6.25	0.04	3.13
Hylaeus hyalinatus	2.30	53.13	2.07	43.75	0.44	21.88
Hylaeus leptocephalus	0.14	9.38	0.06	3.13		
Hylaeus nigritus	2.11	56.25	2.45	59.38	0.40	25.00
Hylaeus pictipes	0.05	3.13			0.04	3.13
Hylaeus punctatus	0.34	12.50	0.50	15.63	1.47	40.63
Hylaeus punctulatissimus	0.10	6.25				
Hylaeus rinki			0.06	3.13		
Hylaeus signatus	0.05	3.13	0.69	15.63		
Hylaeus sinuatus	0.77	31.25	0.50	18.75	0.32	18.75
Hylaeus styriacus			0.06	3.13		
Lasioglossum calceatum	0.48	21.88	0.82	34.38	3.14	71.88
Lasioglossum fulvicorne	0.14	3.13	0.50	12.50	0.20	15.63

Lasioglossum glabriusculum					0.28	3.13
Lasioglossum interruptum			0.06	3.13		
Lasioglossum laticeps	18.13	93.75	23.02	93.75	24.02	96.88
Lasioglossum lativentre	0.14	9.38	0.25	12.50	0.04	3.13
Lasioglossum leucozonium	0.29	15.63	0.38	18.75	1.43	34.38
Lasioglossum malachurum	1.53	34.38	0.31	15.63		
Lasioglossum minutissimum					0.08	6.25
Lasioglossum morio	16.26	87.50	9.22	75.00	6.76	84.38
Lasioglossum nigripes					0.04	3.13
Lasioglossum nitidulum	2.45	59.38	3.95	40.63	1.31	40.63
Lasioglossum parvulum					0.04	3.13
Lasioglossum pauxillum	18.03	93.75	14.62	87.50	10.22	96.88
Lasioglossum politum	0.19	3.13			15.94	93.75
Lasioglossum punctatissimum					0.04	3.13
Lasioglossum pygmaeum					0.04	3.13
Lasioglossum sabulosum			0.06	3.13		
Lasioglossum semilucens			0.06	3.13		
Lasioglossum tricinctum					0.04	3.13
Lasioglossum villosulum	0.14	9.38	0.13	6.25	0.16	6.25
Lasioglossum zonulum			0.56	15.63	0.20	12.50
Lithurgus chrysurus					0.64	28.13
Macropis fulvipes			0.44	12.50		
Megachile centuncularis	0.29	18.75			0.08	6.25
Megachile ericetorum	0.05	3.13			0.20	12.50
Megachile flabellipes					0.04	3.13
Megachile maritima					0.04	3.13
Megachile nigriventris	0.05	3.13	0.13	6.25		
Megachile pilicrus					0.08	6.25
Megachile rotundata					0.40	28.13
Megachile willoughbiella	0.14	6.25	0.31	9.38	1.03	53.13
Nomada fabriciana	0.10	6.25	0.13	6.25	0.04	3.13
Nomada flavoguttata					0.04	3.13
Nomada flavopicta					0.12	6.25
Osmia adunca			0.06	3.13		
Osmia bicornis	0.05	3.13				
Osmia caerulescens	0.19	9.38	0.31	15.63	0.16	12.50
Osmia leaiana	0.10	6.25				
Osmia leucomelana	0.05	3.13	0.13	6.25	0.04	3.13
Osmia mustelina					0.04	3.13
Osmia niveata					0.04	3.13
Panurgus calcaratus					3.78	65.63
Psithyrus barbutellus	0.34	21.88	0.31	15.63		
Psithyrus bohemicus			0.13	6.25		
Psithyrus campestris	0.14	9.38	0.31	12.50		
Psithyrus norwegicus	0.05	3.13				

Psithyrus rupestris	0.19	9.38				
Psithyrus vestalis	0.14	9.38			0.12	6.25
Sphecodes crassus	0.05	3.13			0.04	3.13
Sphecodes ephippius			0.19	9.38	0.16	12.50
Sphecodes ferruginatus	0.24	12.50			0.20	12.50
Sphecodes gibbus					0.04	3.13
Sphecodes hyalinatus	0.05	3.13			0.04	3.13
Sphecodes monilicornis	0.05	3.13			0.20	15.63
Sphecodes niger	0.05	3.13				
Sphecodes reticulatus			0.06	3.13	0.04	3.13
Stelis breviuscula	0.05	3.13	0.13	6.25	0.04	3.13
Stelis punctulatissima	0.10	6.25	0.13	6.25		
Stelis simillima					0.08	6.25
Xylocopa violacea					0.08	6.25

Table S1 C: Bird species (Aves) according to the three study cities. In total 4’120 birds from 63 species were registered at the 96 locations (32 per city; for details per city see Table 2). Steadiness expresses the number of sampling points with the presence of the species. Dominance indicates the fraction (%) of individuals of a single species on the total individual number of birds. This list is based on the same figures as Table S2 in the supplementary material of Fontana et al. (submitted).

All figures in %		**Zurich**		**Lucerne**		**Lugano**	
Scientific name	**Abbreviations**[1]	**Dominance**	**Steadi-ness**	**Dominance**	**Steadi-ness**	**Dominance**	**Steadi-ness**
Accipiter nisus	*Accnis*	0.1	1.0	0.1	1.0		
Acrocephalus scirpaceus	*Acrsci*			0.1	1.0		
Aegithalos caudatus	*Aegcau*	0.9	5.2	2.3	14.6	1.9	10.4
Anas platyrhynchos	*Anapla*	0.1	1.0	0.8	5.2		
Apus apus	*Apuapu*	18.4	29.2	12.2	30.2	7.0	26.0
Apus melba	*Apumel*	0.4	2.1	0.7	2.1	0.1	1.0
Ardea cinerea	*Ardcin*		0.0	0.1	1.0		
Buteo buteo	*Butbut*		0.0	0.1	1.0		
Carduelis cannabina	*Carcan*		0.0			0.1	1.0
Carduelis carduelis	*Carcar*	1.7	15.6	2.5	19.8	3.7	26.0
Carduelis chloris	*Carchl*	4.6	31.3	3.1	27.1	4.5	31.3
Certhia brachydactyla	*Cerbra*	0.3	4.2	0.4	5.2	0.1	2.1
Coccothraustes coccothraustes	*Coccoc*	0.1	1.0				
Columba livia f. *domestica*	*Colliv*	3.3	12.5	1.8	8.3	5.6	22.9
Columba palumbus	*Colpal*	0.2	3.1	1.0	10.4		
Corvus corone	*Corcor*	4.9	29.2	5.0	29.2	6.9	33.3
Corvus monedula	*Cormon*	0.3	1.0	0.7	5.2		
Delichon urbica	*Delurb*	0.1	1.0			2.4	9.4
Dendrocopos major	*Denmaj*	0.6	7.3	0.6	7.3	0.1	2.1
Emberiza cirlus	*Embcir*			0.1	1.0		
Erithacus rubecula	*Erirub*	1.1	12.5	0.9	11.5	1.2	14.6
Fringilla coelebs	*Fricoe*	3.6	27.1	4.8	31.3	3.7	29.2
Garrulus glandarius	*Gargla*	0.4	3.1	0.5	5.2		
Hippolais polyglotta	*Hippol*					0.1	1.0
Hirundo rustica	*Hirrus*	0.2	1.0	0.1	1.0	0.4	4.2
Jynx torquilla	*Jyntor*					0.1	1.0
Larus michahellis	*Larmic*			0.1	1.0		
Locustella naevia	*Locnae*			0.1	1.0		
Loxia curvirostra	*Loxcur*					0.1	1.0
Mergus merganser	*Mermer*			0.1	2.1		
Milvus migrans	*Milmig*	0.2	2.1	0.2	2.1		
Motacilla alba	*Motalb*	0.7	7.3	1.0	10.4	0.9	11.5
Muscicapa striata	*Musstr*	0.6	7.3	1.5	15.6	1.0	10.4
Oenanthe oenanthe	*Oenoen*					0.1	1.0
Parus ater	*Parate*	0.2	3.1	0.6	6.3	0.7	7.3

Parus caeruleus	*Parcae*	3.9	29.2	4.3	27.1	1.4	16.7
Parus cristatus	*Parcri*			0.2	2.1		
Parus major	*Parmaj*	5.9	30.2	6.4	33.3	3.0	25.0
Parus palustris	*Parpal*	0.1	1.0	0.3	3.1		
Passer domesticus	*Pasdom*	24.1	33.3	16.7	30.2		
Passer hispaniolensis italiae	*Pashis*					29.4	33.3
Passer montanus	*Pasmon*	0.2	1.0	0.1	1.0	0.4	2.1
Phalacrocorax carbo	*Phacar*			0.1	1.0		
Phoenicurus ochruros	*Phooch*	1.8	19.8	3.3	29.2	1.2	14.6
Phoenicurus phoenicurus	*Phopho*	0.2	2.1	0.1	1.0	1.8	18.8
Phylloscopus collybita	*Phycol*	0.5	5.2	0.9	10.4	0.1	2.1
Phylloscopus trochilus	*Phytro*					0.1	1.0
Pica pica	*Picpic*	2.3	19.8	1.4	11.5		
Picus viridis	*Picvir*	0.1	1.0	0.1	1.0	0.1	2.1
Ptyonoprogne rupestris	*Ptyrup*					0.4	2.1
Pyrrhula pyrrhula	*Pyrpyr*			0.1	1.0		
Regulus ignicapillus	*Regign*	0.6	6.3	1.6	15.6	0.8	9.4
Regulus regulus	*Regreg*	0.2	1.0				
Saxicola rubetra	*Saxrub*					0.1	1.0
Serinus serinus	*Serser*	0.6	8.3	1.5	15.6	2.7	25.0
Sitta europaea	*Siteur*	0.7	8.3	1.0	10.4	0.6	7.3
Streptopelia decaocto	*Strdec*	1.9	14.6	0.6	5.2	2.7	19.8
Sturnus vulgaris	*Stuvul*	3.4	20.8	3.3	19.8	1.4	10.4
Sylvia atricapilla	*Sylatr*	3.2	21.9	3.3	28.1	4.8	29.2
Troglodytes troglodytes	*Trotro*	0.4	3.1	0.4	5.2	0.4	4.2
Turdus merula	*Turmer*	7.1	32.3	12.5	33.3	8.1	32.3
Turdus philomelos	*Turphi*			0.1	2.1		
Turdus viscivorus	*Turvis*			0.1	1.0		

[1] see Fig. S3 A, B, C

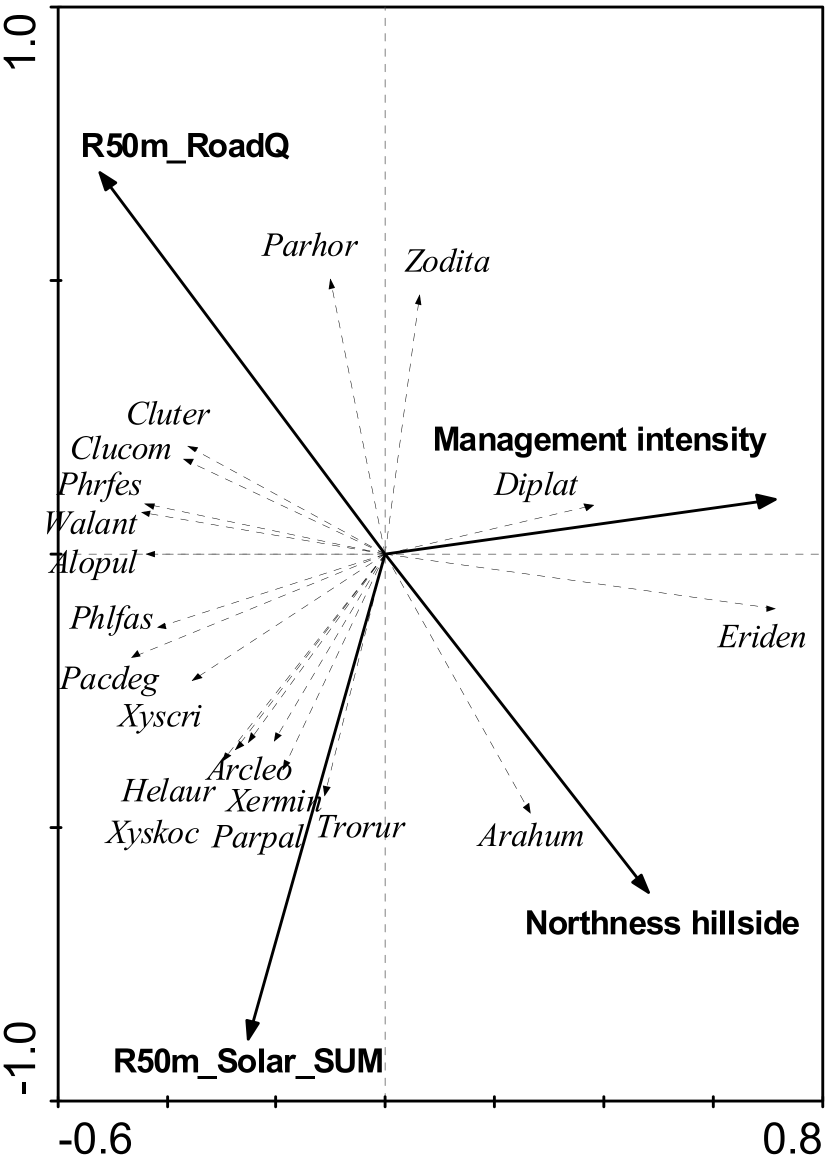

Fig. S2 A: Biplot of species community analysis of spiders (Araneae) in Zurich (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 A.

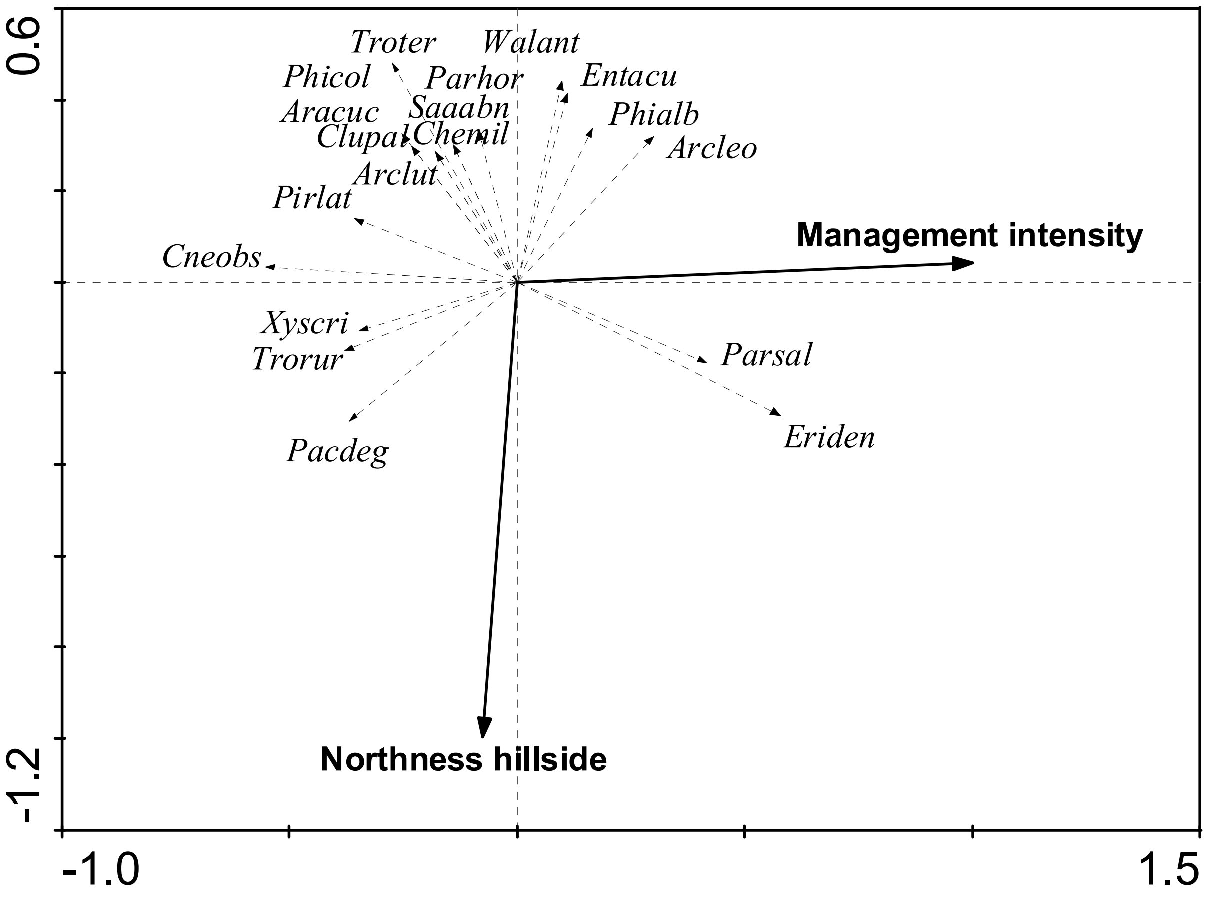

Fig. S2 B: Biplot of species community analysis of spiders (Araneae) in Lucerne (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 A.

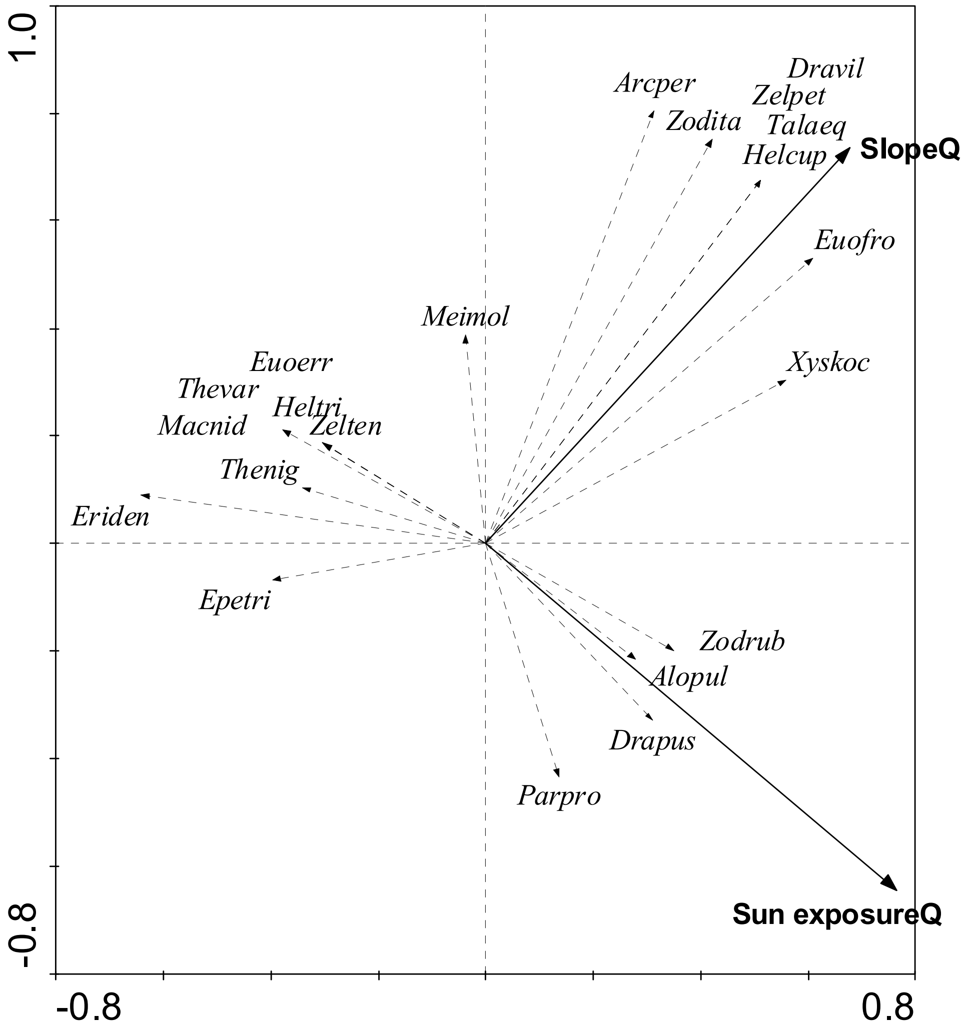

Fig. S2 C: Biplot of species community analysis of spiders (Araneae) in Lugano (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 A.

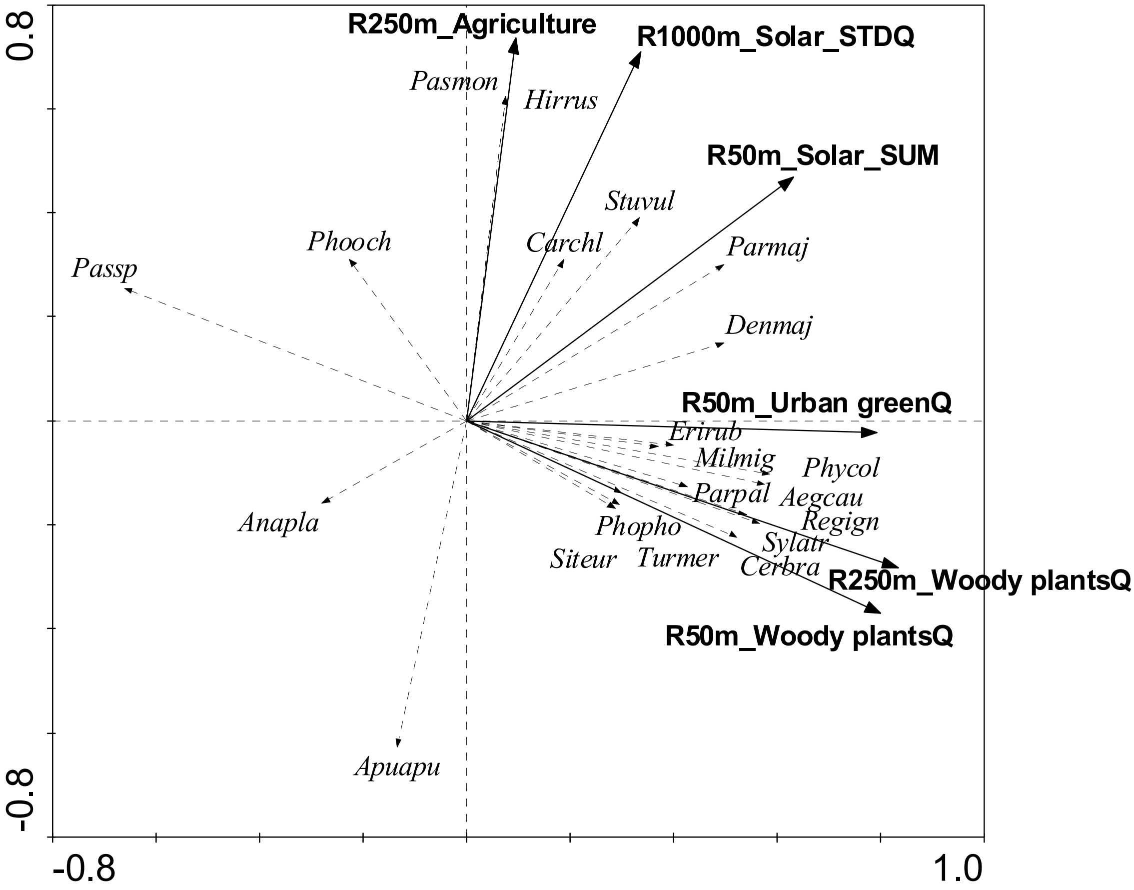

Fig. S3 A: Biplot of species community analysis of birds (Aves) in Zurich (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 C.

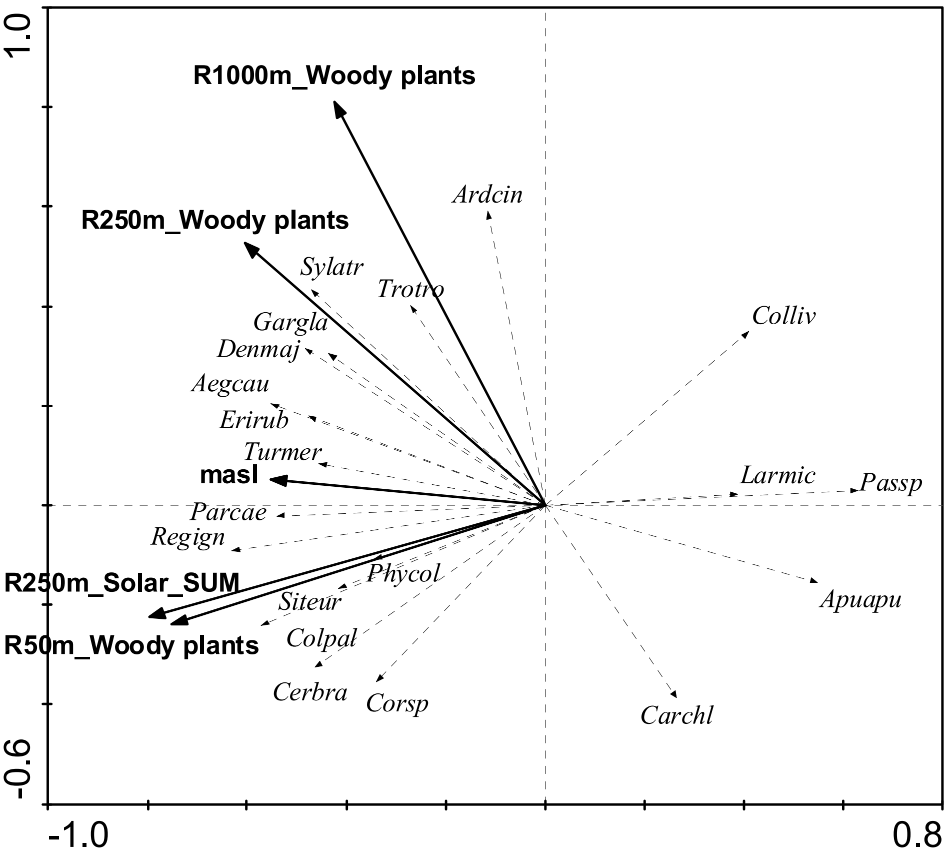

Fig. S3 B: Biplot of species community analysis of birds (Aves) in Lucerne (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 C.

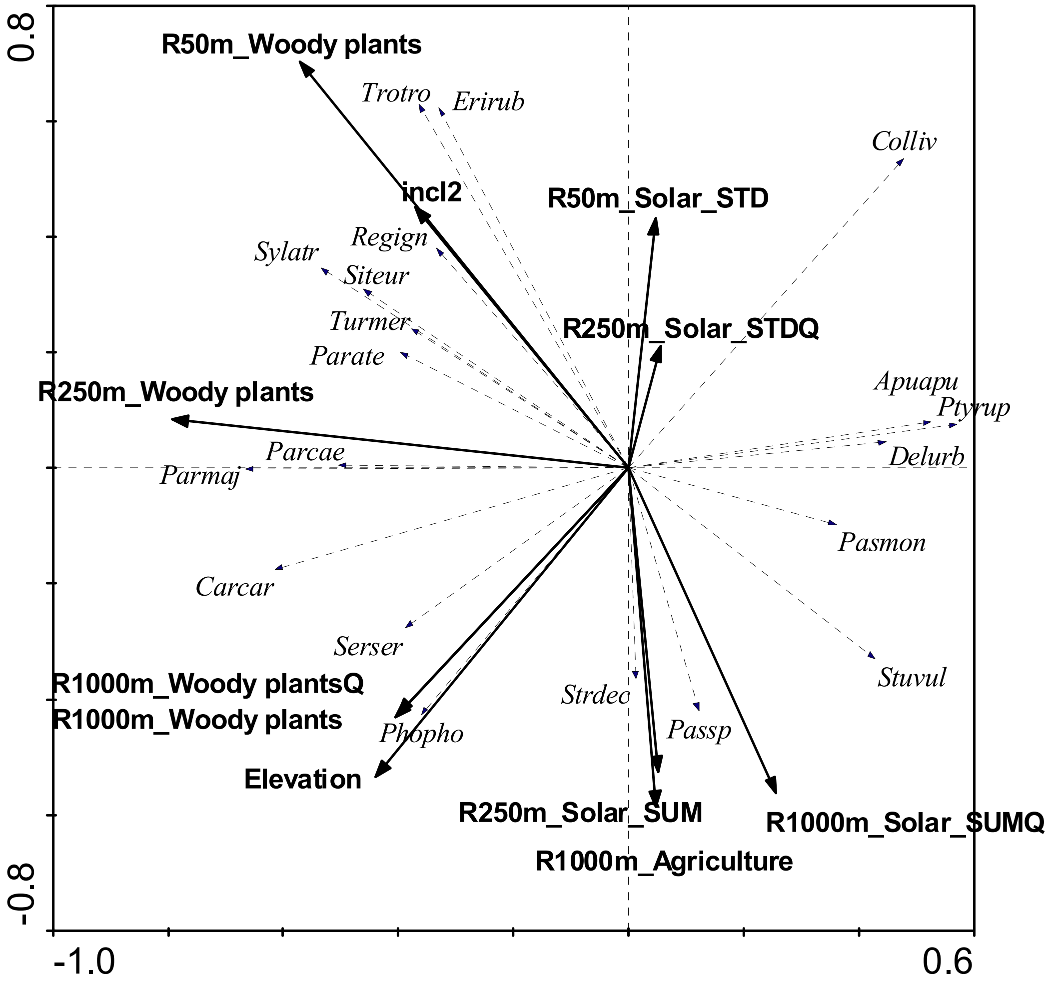

Fig. S3 C: Biplot of species community analysis of birds (Aves) in Lugano (RDA, for details see methods) showing the first canonical axis on the x-axis and the second on the y-axis (n = 32). Selected environmental variables in bold arrows; for visibility only the species most correlated to the first two canonical axes are shown (dashed arrows); abbreviated species names (i.e. 3 letters of the genus and 3 letters of the species) see Table S1 C (*Passp=Passer spec.=P. domesticus* and *P. hispaniolensis italiae*).

References cited in supplementary material

Fontana S., T. Sattler, F. Bontadina, and M. Moretti. submitted. How to manage the urban green to enhance bird species richness and diversity. Biological Conservation.

5

Bat’s exploitation of cities: the importance of spatial and environmental variables

Bat’s exploitation of cities: the importance of spatial and environmental variables

T. Sattler[1, 2], M.K. Obrist[3], R. Arlettaz[2], M. Moretti[1], F. Bontadina[2,4]

[1] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[2] Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[3] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

[4] SWILD – Urban Ecology & Wildlife Research, Wuhrstrasse 12, CH-8003 Zurich, Switzerland

Manuscript in preparation

5.1 Abstract

1) The worldwide expansion and densification of urban areas has caused major concern for the conservation of biodiversity. While the high human impact in urban areas has strongly affected populations of ground-dwelling animals and even birds, the effect on bats that form colonies and exploit scattered habitat patches in large home ranges remains unknown.

2) We recorded bat occurrence and activity levels with repeated bioacoustic surveys in two Swiss cities at 64 sampling locations in both the reproduction and post-reproduction seasons. Bat species were determined by pattern recognition algorithms which were visually controlled.

3) We used the AIC approach to select variables from a set of 30 environmental predictors to explain echolocation activity. Combining the identified environmental variables, the spatial Moran Eigenvector (MEM) variables and one predictor for food abundance in a variation partitioning analysis determined the relative importance of the three components.

4) Fourteen bat species (half of the Swiss bat species) were recorded in the cities with six species (*Hypsugo savii, Nyctalus noctula, Pipistrellus kuhlii, P. nathusii, P. pipistrellus* and *P. pygmaeus*) occurring regularly. Of these, two species (*H. savii, P. kuhlii*) have successfully invaded the study cities north of the Alps only in the last two decades, probably profiting from the warmer temperatures in cities.

5) We identified many variables with often strong effect sizes to explain activity of bat species and call type groups in both cities. Variation partitioning revealed high proportions of up to 44% variance in bat activity explained by the three components (environment, spatial and food). A significant portion was explained by the spatial variables, in the smaller city they explained in combination with the environmental variables.

6) We explain the high variability in the selected environmental variables with the opportunistic foraging behaviour, which changes the aerial hawkers to generalists, and with the colonising species that exploit non-saturated habitats. The major contribution of spatial components, particularly in the reproduction season, underlines the importance of spatial aggregation in social animals.
7) Bats, with their high level of social organisation, share common maternity roosts and offer a unique model to study the interplay of spatial and environmental variables.

Keywords

Chiroptera, *Hypsugo savii, Pipistrellus kuhlii*, urban, habitat association, food, Switzerland, Moran Eigenvector maps, variation partitioning

5.2 Introduction

Urbanisation is characterised by the densification and expansion of already populated areas and has led to dramatic transformations of landscapes (Vitousek et al. 1997, Liu et al. 2003). Despite this worldwide (Grimm et al. 2008) process that happens at accelerating velocity (Likens 1991), urban areas still function as ecosystems and contain the same components (plants, animals, water, soil, etc.) and processes (energy, nutrient, water cycles) as areas less densely populated by humans (Sukopp and Wittig 1998, Zipperer et al. 2000, McDonnell et al. 2009). In recent decades, urban areas have been recognized as important habitats hosting a rich biodiversity of many different taxonomic groups such as plants, (e.g. Sukopp et al. 1979, Thompson et al. 2004), arthropods (e.g. Klausnitzer 1988, Smith et al. 2006, Sattler et al. submitted) and birds (e.g. Marzluff 2001, Fontana et al. submitted). Human-dominated areas have also been shown to support several bat species (Gaisler et al. 1998, Gehrt and Chelsvig 2004, Avila-Flores and Fenton 2005, Hourigan et al. 2008) but the ecology of urban bats remains a field that is surprisingly little studied. Initially, urban areas were described as bat-poor environments (Kurta and Teramino 1992), but recently it has been shown that such a classification might be context-dependent. Often more bat species live in urban than adjacent agricultural areas (Gehrt and Chelsvig 2003) and bats may benefit in several ways from urban areas. Bats use buildings to roost, for mating or hibernation (Dietz et al. 2007) and forage over illuminated industrial areas and near street lamps that attract and accumulate insect prey (Rydell 1992, Blake et al. 1994). In addition, bats generally may profit from more favorable climate conditions in cities. Some species may even populate areas that previously did not belong to their natural range, i.e. the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne (Parris and Hazell 2005), or Kuhl's bat (*Pipistrellus kuhlii*) in Central Europe (Dietz et al. 2007) due to warmer temperatures in cities and milder winters.

In order to understand the presence or absence of bat species in urban areas it is necessary to identify the factors that determine their occurrence.

Bat – habitat associations are investigated by an increasing number of studies in non urban environments (e.g. Furlonger et al. 1987, Vaughan et al. 1997a, Arlettaz 1999, Bontadina et al. 2002, Ford et al. 2005, Sattler et al. 2007) and a smaller number are undertaken within cities (Gaisler et al. 1998, Lesinski et al. 2000, Gehrt and Chelsvig 2004, Scanlon and Petit 2008b). The studies are often limited to investigating only one or few of the many factors that affect bat distribution and activity. The relative importance of the different variables types affecting bats (habitat, food, spatial, climate, topography, moon and artificial light, time in the night) remains unknown. Additionally, it is important to measure habitat variables on different scales (i.e. landscape vs. microhabitat scale; Johnson 1980, Wiens 1989), however this aspect is only rarely investigated in bats (but see Gehrt and Chelsvig 2003, Pinto and Keitt 2008, Popa-Lisseanu et al. 2009).

Distributions of species are spatially organized (Wiens 1989, Fortin and Dale 2005). The spatial patterns are essentially created by two different processes: 1) autogenic (biotic) processes (i.e. dispersal, growth, mortality, interspecific competition, social organization that itself is spatially structured). 2) exogenous processes (species respond to environmental variables that themselves are spatially structured). Principal Coordinates of Neighbor Matrices (PCNM)(Borcard and Legendre 2002, Borcard et al. 2004) and Moran’s eigenvector maps (MEMs; Dray et al. 2006) are used to model the autogenic spatial component of a species’ distribution. PCNM variables actually form a sub-family of the MEM variables, since both are eigenvectors obtained from spatially weighted connectivity matrices of sampling locations used to model both uni- (i.e. species richness) and multivariate (community composition) data (Legendre et al. 2009, Sattler et al. in preparation). Such sophisticated spatial variables have not as yet been included into the analysis of the occurrence of social animals such as bats.

In the present study, we aim to explain bat occurrence in urban areas by including environmental (habitat measured in different radii and topographical), food availability, and spatial variables into the analysis while at the same time controlling for temperature and time of night of the survey. Food availability is often mentioned as a possible limiting factor for bats causing niche differentiation (Giannini and Kalko 2004, Siemers and Schnitzler 2004), but food limitation has rarely been proven with published data, and especially not for aerial hawking bats (Grindal and Brigham 1999, Avila-Flores and Fenton 2005). As an elusive and nocturnal group, bats are difficult to monitor, especially when foraging. Thanks to advances in both fields, the development of technical echolocation devices (Parsons and Obrist 2004) and call recognition of species (Zingg 1990, Vaughan et al. 1997b, Russo and Jones 2002, Obrist et al. 2004b), bat call surveys have become a popular tool to study bat ecology. In temperate zones most species are identified with high probabilities by their echolocation calls. In our study, we use repeated echolocation surveys to focus on the following two research questions: A) Which environmental variables influence presence and activity of the different urban bat species and what is their effect size? B) What is the relative contribution of environmental, food and spatial components to explain activity of urban bats?

5.3 Methods

5.3.1 Study sites and sampling design

Data were collected in the two Swiss cities of Lucerne and Zurich (58'000 and 371’000 inhabitants, respectively) in Northern Switzerland (408m and 436m asl, respectively). They experience a temperate climate (average January temperature 1°C, July 17°C). Bat calls were recorded at 64 sampling locations (32 in each city), which were chosen along a gradient of impervious area (sealed and built area, see below). The sampling locations were in private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings (detailed locations in Germann et al. 2008). A minimum distance of 250 m between sampling points inhibited spatial auto-correlation, which was confirmed using the Moran’s Index (Legendre and Legendre 1998); data not shown). The same minimum distance of 250 m was kept to the city border in order to reduce edge effects.

5.3.2 Bat recordings and call identification

Bat recordings were performed in two study seasons, the reproduction season (20/6 - 5/8/2007) and the post-reproduction season (12/8 - 21/9/2007). The two species *Nyctalus noctula* and *Pipistrellus nathusii* are known to only rarely reproduce in Switzerland (even though the latter species has undergone a range expansion in the last decades) but individuals (mainly males) still pass the summer in Switzerland (Dietz et al. 2007). Thus, reproduction season depicts the time period only for these two species. In each season, bat call recordings were replicated twice per sampling location. Recordings were started half an hour after sunset, continued for 45 minutes, and were operated sequentially at different locations during the night. In this way, two self developed recording devices (Obrist et al. 2004b) were simultaneously operated so that eight recording locations were sampled per night. Bat activity is not continuous during the night, which in turn affects detection probability (Gaisler et al. 1998, Scanlon and Petit 2008b) so the order of sampling points during one night was alternated between the start and end of each replicate.

Two custom-built microphones (frequency response ±3 dB from 20-120 kHz; Ultrasound Advice, London, UK) were installed within a radius of 25m around the central point of the sampling location. Microphones were installed 1 m above ground pointing 45° upwards and at opposite directions, and cable-connected to the central recording unit. Bat echolocation was digitally recorded with PCMCIA data acquisition cards (PCCARD-DAS16/330, Measurement Computing Corporation, Middleboro, MA, USA) in Apple PowerBook computers. Looped recordings of 10 s duration were driven by custom-made software (Obrist et al. 2004b) switching between the two microphones. As there was a small data storage time gap between each recording loop, we ended up with approx. 45 seconds of recording time per minute (duty cycle of 75%), resulting in effective 33.75 minutes of operation per site and night. Sequences were analysed offline in the lab. A peak-detection algorithm scanned the recorded sequences after high-pass filtering at 7.5 kHz. We used custom written software (Obrist et al. 2004a, Obrist et al. 2004b) to automatically identify echolocation calls of bat species. Sequences were cut into single echolocation calls from which we calculated spectrograms, which were synergetically compared against five sets of prototype-spectrograms of known species and thus classified to species. These five sets had previously been identified to optimally recognize 26 Swiss bat species (Obrist et al. 2004b) with an average correct classification rate of 86%. In a probabilistic approach, of the five classifications at least four had to pass a given quality standard and of these, at least three classifications had to point to the same species. Spectral (highest, lowest, main frequency) and temporal (duration) parameters of a classified signal were then validated against a parametric database of the classified species. Only if pattern recognition and call parameter control passed all tests for the species in question, a signal was considered as recognized. After automatic recognition, all sequences of questionable probability (e.g. multiple species and/or only few calls recognized) were visually screened for errors and manually classified to species, after comparing spectral and temporal parameters with published data for Switzerland (Zingg 1990, Obrist et al. 2004b). The dependent variable, bat activity, was calculated as the number of minutes with echolocation activity per 45 minute session and species. Activity per species and the activity of call sequences that could not be attributed to species but to genus or species group level were summarised in call type groups. We distinguished between three call type groups: frequency modulated (FM) – constant frequency (CF) call types with the frequency of maximum energy above 32 kHz (FM – CF > 32kHz) belong to the genus Pipistrellus and Hypsugo; FM – CF call types with the frequency of maximum energy below 32 kHz (FM – CF < 32kHz) belong to the genus Eptesicus, Vespertilio and Nyctalus; FM call types belong to the genus Myotis and Plecotus. Call types reflect a similar foraging niche (Neuweiler 1989): FM-CF call types >32kHz forage around and in close distance to structures such as bushes, trees and street lamps. FM – CF call types <32 kHz rather hunt in open, unstructured air space. FM call types usually forage within the vegetation (exception: *M. daubentonii* mainly hunts above the water surface (Dietz et al. 2006)).

5.3.3 Environmental predictors

An overview on the four data sets used as environmental variables is presented in Table 1. The data set 'local' consists of four topographical variables (Elevation, Slope, Eastness, Northness; all obtained from digital elevation model) and the minimal distance to the nearest large water body (obtained from GIS maps). The other three data sets represent circular analysis of the land cover information (Buildings, Roads, Urban Green) and variables obtained from Digital Surface Models (woody plants) measured on three different radii around the sampling points (data set on 50m radius ('R50m'), on 250m radius ('R250m'), on 1000m radius ('R1000m')). The land cover variables are measured as frequencies (%) obtained from theme-specific layers of the topographic map 1:25'000 of Switzerland and did not sum to 100%. Digital Surface Models for Switzerland (airborne laser scanning methods LIDAR) depict the elevation of the Earth's surface including vegetation and buildings (Artuso et al. 2003) using airborne laser scanning methods. These data are available in cell sizes of 2.5 x 2.5m and have a vertical accuracy of ±0.5 m in open terrain ±1.5 m in terrain with vegetation. Based on this digital surface model, we obtained an index for woody plant cover (trees and bushes). All cells higher than 1m that are not depicted as buildings in the building layer of the land cover layers of the topographic map 1:25'000 were classified as woody plants. Selection of location was effected along the minimum and maximum values of the gradient 'impervious area' (Lucerne: 6.5-86.3%, Zurich: 2.5-91.8%; 100 % = 0.79ha).

To allow for curvilinear effects of the explanatory variables, we incorporated linear and quadratic terms for Elevation, Slope and the cover variables. In total we had seven predictor variables for the environmental data set 'local variables' and eight for the three data sets 'R50m', 'R250m' and 'R1000m'.

5.3.4 Food abundance predictor

At each of the 64 study locations, flying invertebrates were sampled using so-called combination traps (Duelli et al. 1999). Arthropods were sampled during seven weeks in the period of highest arthropod abundance in Central

Europe (Duelli et al. 1999) which means that traps were opened between June 13th and 15th 2006 (depending on city) and then emptied weekly until closure between August 1st and 3rd 2006. One index of arthropod biomass was determined on volume (ml). We assumed that the relative arthropod biomass per sampling location remains unchanged over the the season. More information on arthropod sampling is found in Sattler et al. (submitted).

5.3.5 Spatial predictors

Moran eigenvector maps (Dray et al. 2006) were used to obtain spatial predictor variables that can be used in regression or ordination. MEMs represent the generalized form of the previously developed principal coordinates of neighbor matrices (PCNM; Borcard and Legendre 2002). Both methods use the eigenfunctions of the spatial configuration (= connectivity) matrices. The resulting variables (eigenvectors) are orthogonal to each other, so they are additive in scale-specific models (Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). MEM variables are more flexible to geographically irregular sampling schemes, as it was the case in our cities, and a wider array of connectivity matrices can be applied than in the classical PCNM approach. According to Dray et al. (2006), we proceeded as follows:

1) We obtained a Connectivity Matrix ($\mathbf{B} = [b_{ij}]$) based on coordinates of sampling locations. We used Delaunay Triangulation (Legendre and Legendre 1998) to define neighboring locations. Thereby we excluded connections that cross lakes, as we assume that spatial processes crossing the open water are insignificant in our context.

2) We then computed a Euclidean distance matrix ($\mathbf{D} = [d_{ij}]$) between neighboring locations and derived a weighting matrix $\mathbf{A}$ where $[a_{ij}] = 1/[d_{ij}]$.

3) The Connectivity Matrix $\mathbf{B}$ is weighted according to this distance, meaning that locations that are closer together are given greater weight ($1/d$) in the analysis. The final, spatial weighting matrix $\mathbf{W}$ results from the Hadamard (i.e., term-by-term) product of $\mathbf{B}$ and $\mathbf{A}$.

4) Moran’s eigenvectors and eigenvalues are calculated on the spatial weighting matrix **W**. The resulting variables are continuous.
5) The eigenvectors with positive eigenvalues, representing positive spatial autocorrelation, were included in data (see below) as spatial predictor (MEM) variables.

This procedure yielded nine MEM variables in both cities. The MEM variables associated with small eigenvalues consist of fine waves with high frequency patterns and represent local structures while those associated with large eigenvalues exhibit broad-scale frequency and represent scales on the maximum distances between sampling locations for each city (Lucerne = 4.3 km, Zurich = 6.2 km; Borcard and Legendre 2002, Dray et al. 2006). MEM eigenfunctions were created with R-package spacemakeR (Dray 2008).

5.3.6 Data analysis

Fig. 1 gives an overview on the different steps of analysis and the data sets used. We used the R-language (R Development Core Team 2007) for all statistical analysis with several libraries as indicated. Bat activity data is Poisson distributed and the two activity measurements per season are repeated in sampling locations. Therefore, we used Generalised Linear Mixed Effect models (lmer function of R-library lme4 (Bates et al. 2008) to relate bat activity per species or species group to the environmental and spatial variables. It is well known that bat activity is affected by both the time after sunset and air temperature (Gaisler et al. 1998, Scanlon and Petit 2008b). Thus, we controlled for the effect of these variables and included them as co-variables in all a-priori models mentioned below.

Question A: We analyzed activity of each bat species and species group with the environmental data sets measured on the four different radii, and for the reproduction and post-reproduction seasons and for the two cities Lucerne and Zurich. For each of the four environmental variable sets individually, we selected variables based on an information-theoretic approach in which a-priori models were ranked according to their support by the data using Akaike weights obtained from the Akaike’s Information Criterion corrected for small sample size, (AICc; Burnham and Anderson

2002, Johnson and Omland 2004). The number and composition of the a-priori models depended on the variables of the environmental data set analysed (Supplementary material) and represents all possible combinations of the variables included and the Null model (no environmental variables included, assuming random distribution). In this way, we defined 32 candidate models for the local data set and 16 candidate models for the three data sets R50m, R250m, R1000m (Supplementary material). The variables of the best models within Δ AICc of 2 were selected as the most parsimonious variables which were subsequently included into variation partitioning.

Question B: We applied variation partitioning (Borcard et al. 1992, Borcard and Legendre 1994) to determine the fraction of explained variation in bat activity by the three main components environmental, food and spatial, both individually and in combination. For the environmental information we used the previously AICc-selected variables. For the food information we used the single variable on biomass of flying insects. For the spatial information we used the X an Y coordinates of the sampling locations and the MEM variables. Again, relevant MEM variables were selected with an information theoretic procedure and Δ AICc <2. Variation partitioning is implemented in the Vegan package (Oksanen et al. 2008). We report the variation explained in each RDA model as the adjusted R^2 (R^2_a) which takes the number of predictor variables and sample size into account to prevent the inflation of R^2 values (Peres-Neto et al. 2006). When a negative R^2_a was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006) meaning that not all fractions of one variation partitioning always sum to 100%.

5.4 Results

In total, we recorded 3474 minutes of bat activity in Lucerne and 1775 minutes of bat activity in Zurich. Of these total activity minutes, 2667 for Lucerne and 1355 for Zurich could be attributed to a total of 14 species. Twelve species were identified in both cities (*Eptesicus nilsonii, Hypsugo* *savii, Myotis daubentonii, M. mystacinus, Nyctalus leisleri, N. noctula, Pipistrellus kuhlii, P. nathusii, P. pipistrellus, P. pygmaeus, Plecotus austriacus, Vespertilio murinus*). *Eptesicus serotinus* was recorded in Lucerne only and *Myotis myotis* in Zurich only.

Nevertheless, more than half of these species were identified at only small activity levels and therefore have to be considered as occasional to exceptional inhabitants of the cities. Six species in Lucerne and five species in Zurich yielded sufficient numbers (2603 Lucerne, 1318 Zurich) for statistical analysis (Table 2). They represent 97.6% (Lucerne) and 97.3% (Zurich) of the total activity minutes attributed on species level.

Activity per call type groups summarises the activity per minute of call sequences that were attributed to species, genus or species group level and yielded a total of 2400 activity minutes in Lucerne and 1378 in Zurich. The call type group frequency modulated (FM) – frequency constant (CF) call types above 32 kHz (genus Pipistrellus and Hypsugo) dominate both cities with 90.6% of call type groups in Lucerne and 96.7% in Zurich, respectively (Table 2).

AICc-selection procedures identified the relevant environmental variables from the four data sets (local, R50m, R250m, R100m). Results indicate high variability in both the identified variables and their respective effect sizes for the different species and call type groups. Often, different variables were chosen for the same species depending on the city and the season under study (Tables 3A, 3B). In Lucerne, generally more environmental variables were selected and thus affect bat activity. Increasing distance to water has a generally negative influence on bat activity. Additionally, land cover variables measured on the R50m show considerable effect sizes for many species and call type groups in this city. With the exception of *N. noctula*, all species show a positive correlation between activity and building area, however, most Pipistrellus species prefer an optimum level of building area after which their activity level drops again. The estimates of *P. kuhlii* and *H. savii* have large standard error terms (SE) in this squared building variable, so their relationship is unclear. These two, originally Mediterranean species also show a clear avoidance of woody plants (trees and bushes) on this radius in Lucerne. The effect sizes of the selected land cover variables on both larger radii (R250m and R1000m) are minor and are afflicted with comparatively large SE terms.

In Zurich, the local information and especially the land cover variables of R1000m are selected most. Habitat cover of the R50m and R250m were chosen only by *P. pipistrellus* and *N. noctula* in the reproduction season. The large effect sizes for the latter species are imprecise, as indicated by the large SE, which is probably due to low sampling frequency. The activities of several species positively correlate with increasing road area on the largest radius (*N. noctula* (reproduction season), *P. nathusii* (both seasons), *P. pipistrellus* (reproduction), call type FM-CF < 32kHz (both seasons)), but they all also reach an optimum level of road area as indicated by the effect sizes for the quadratic term (Table 3B).

Variation partitioning shows the relative contribution of the three explanatory data sets environmental, food and spatial variables. In Lucerne, these variables explain in total between 13.5% and 42.4% of the total variation per species or call type groups in the reproduction season and between 5.1% and 42.9% in the post-reproduction season (Table 4A). In Zurich, the same figures range between 0% and 43.8% in the reproduction season and between 0% and 25.2% in the post-reproduction season (Table 4B). The total explained variation was for most species higher in the reproduction season than in the post reproduction season. In Lucerne, total variation explained was on average 28.6% in the reproduction season and 24.0% in the post-reproduction season. In Zurich, the average total variation explained was more than double (30.3%) in the reproduction season than in the post-reproduction season (14.0%). This indicates that the enclosed variables are better suited to describing foraging behavior in the reproduction than in the post-reproduction season, or in other words, bat occurrence is less structured in the post-reproduction season.

The total explained variation can be split in the relative contributions of the food, environmental and spatial components. In both cities, food availability, including all combinations with the two other data sets, explains little of the variation for all species (Tab. 5). In the reproduction season the mean values were 3.5% in Lucerne and 4.0% in Zurich and in the post-reproduction season they were 3% and 0.8%, respectively.

The relative contribution of the remaining environmental and spatial data sets to explaining total variation of bat activity differs between the two cities (Table 4A, 4B). In the small city of Lucerne, the activity of most species and call type groups were explained best by the purely environmental variables in both seasons (reproduction season mean 16.4%, range 0.7-30.4%; post-reproduction season mean 9.1%; 2.5-19.2%). However, also the spatially structured environmental (SSE) component explains considerable amounts for all species in at least one season (up to 18.2% in the reproduction season and up to 18.7% in the post-reproduction season). In the larger city of Zurich we observed a shift in the importance of the components between seasons. While a major part of bat activity of the reproduction season was explained by the purely spatial component (mean value 14%; range 0-22.2%), in the post-reproduction season the spatial component had only a small influence (mean 3%; 0-8%) and most information was either explained by the SSE or the purely environmental component (Table 4B). This result is possibly indicating that the spatial fusing effect of bat activity through maternity roosts becomes lost in the post-reproduction season.

5.5 Discussion

We explain bat activity not only by environmental variables but also include frequently neglected variables, such as spatial MEM variables and an estimate of food availability, into variation partitioning to explain bat activity. This approach explains up to 44% of the total variation in bat activity and enables the estimation of the relative importance of these components. The high proportion of explained variation in bats is largely due to an important spatial component which is in strong contrast to a similarly structured study with community composition of arthropods and birds, where the spatial component was virtually absent (Sattler et al. in preparation). The finding that total explained variance is larger in the reproduction than in the post-reproduction season indicates either a) that the higher energy demand caused by lactation drives the lactating females to select more (profitable) foraging habitats and/or b) that hunting female bats are more experienced in selecting (profitable) foraging habitats than the young bats. In the post-reproduction (and thus post lactation) season, the energy demand puts less pressure on the females to be highly efficient and/or the inexperienced young are less selective in their habitat choices.

The spatial dimension explained a significant fraction of the variation in bat activity. This is best explained by the distribution of roosts in space where these social animals aggregate, especially the maternity roosts during the reproduction season. A suitable foraging habitat closer to a bat roost is expected to have a higher probability of being visited by a given species (Bontadina et al. 2002). For example, even fast-flying bats such as *Tadarida australis* mostly forage within a close range (a few km for this species) of roosts (Rhodes and Carferall 2008).

While we find significant portions of explained variations that are explained through space in both cities, the relative attribution to the different components differs between the cities. The purely spatial component plays an important role in larger city of Zurich, whereas in the smaller city of Lucerne the explained spatial information is contained in the spatially structured (SSE) component (Table 4A, 4B). The substantial SSE component in Lucerne indicates that the explained spatial information could be explained by either the autogenic spatial structure (spatial distribution of roosts) that also correlates with the bat relevant environmental variables or by the bat relevant environmental variables that themselves are spatially organized. The cause for this difference is not clear, although it is possibly linked to the spatial dimensions of the cities. The urbanized area (including suburbs) is roughly four times larger in Zurich than in Lucerne and the smaller spatial extent may cause the bat-relevant environmental variables in Lucerne to be spatially structured and thus explain most of the spatial structure caused by autogenic variation. Nevertheless, this question of causality does not change the outcome that bats in both cities are spatially organised.

The spatial portion (purely spatial and SSE components) are larger in the reproduction season than in the post-reproduction season for many species and call type groups. This decrease from the reproduction to the post-reproduction season is explained in that the spatial dependency on the (maternity) roosts is higher in the reproduction than in the post-reproduction season when the more independently foraging bats may use more single roosts that are dispersed in a wider area.

The absence of explained variation by the purely food fraction or any combination including the food component, may be explained by two alternative hypotheses: A) Food biomass is not a factor delimitating activity of the observed urban bat species (aerial hawkers) from June to September. We recorded food availability and bat activity in peak season where abundance of arthropods may be some order of magnitude higher compared to the less abundant times of the year. B) The method applied to measure arthropod biomass (abundance) does not measure the bat relevant arthropod biomass. It is possible that the trapping method does not correctly capture night-active insects that function as bat prey. Nevertheless, we must remember that every method used to estimate insect biomass, such as malaise and light traps (Bontadina et al. 2008, Scanlon and Petit 2008a) and photographic "trapping" methods (Avila-Flores and Fenton 2005), has its limitations. Alternatively, local food biomass might be highly biased by artificial light at night. In this case, food abundance of a larger surrounding than our biomass measure would influence the attractiveness of recordings sites for bats.

In the two Swiss cities, we identified call sequences belonging to 14 of the 28 bat species currently living in Switzerland, which accounts for approximately half of the mammal species that have been recorded in the city of Zurich (Ineichen and Ruckstuhl in press). Another intensive bioacoustic survey of diverse woodlands in Southern Switzerland yielded only 6 to 12 species (Obrist et al. in review). However, eight of our 14 species were recorded in low activity numbers and must be regarded as occasional to exceptional inhabitants of the two cities. Two species have invaded cities North of the Alps only in the last years: In the twenty years since appearance *P. kuhlii* has reached strong populations in both cities while the regular presence of *H. savii* was newly found in this study. The six species regularly encountered in the study cities (*Hypsugo savii, Nyctalus noctula, Pipistrellus kuhlii, P. nathusii, P. pipistrellus* in both cities and *P. pygmaeus* in Lucerne) all belong to the FM-FC call group which hunt either in the open air space or near structures such as woody plants, street lamps and buildings (aerial hawkers). Species from the large genus Myotis (nine species) are mostly gleaning specialists or hunt within the vegetation. This species group are either rare or absent in the cities, indicating that only aerial hawkers actually benefit from urban areas.

For foraging habitat selection, the following general patterns can be recognised. In Zurich, land cover variables of the radius 1000m are selected most, which possibly reflects that all study species have home ranges in at least this order of magnitude. Even the small bats of the genus Pipistrellus forage up to maximum distances of 0.7 – 2.3 km (*P. pygmaeus*) and 1.2 – 3.4km (*P. pipistrellus*) from their roost (Nicholls and Racey 2006). The finding that, on this radius, the activities of several species positively correlate with increasing road area reflects that street lamps attract insects which provide an easily accessible and abundant food source for these aerial insectivores. In Lucerne, the negative correlation of bat activity with increasing distances from large water bodies emphasises the importance of this habitat type in provisioning food biomass for bats. In the same city, species from the genus Pipistrellus and *H. savii* show a positive correlation with increasing building area (reaching an optimum level) but show opposed preferences of trees and bushes on the R50m. While the activity of *P. nathusii* and *P. pipistrellus* increases with increasing woody vegetation, the activity of *P. kuhlii* and *H. savii* decreases. *P. kuhlii* is known as a species that uses urbanised areas as optimal foraging grounds (in Southern Switzerland successfully competing with *P. pipistrellus*; (Haffner and Stutz 1985/86) or even using cities as stepping stones to colonise regions North of the Alpine arch in the last decades (Dietz et al. 2007). *H. savii* originally roosted in rocks and cliffs of the Mediterranean but has occupied also cities in this area and has moved northwards in the last warm decade (Dietz et al. 2007). Probably highly built areas with an open air space represent an artificial but suitable landscape for this species. We hypothesise that this species starts to use an ecological niche that has so far not been occupied during night time. During day time in central Europe, two bird species, *Apus apus* and *A. melba*, which both originally occurred in the Alps in the similar rocky environment as *H. savii*, use the open air in highly built area as foraging areas. The absence of selected variables by *H. savii* in Lucerne could be caused by it being an expanding species whose population is not yet saturated. In this case we would expect that many optimal places are still unoccupied making it impossible to identify clear habitat selection patterns.

Results from the repeated measures in both sampling seasons demonstrate a high variability of the activity measures. Bats seem to react very flexibly to supposed changes in local insect availability. Therefore it is not surprising that results on bat – foraging habitat associations of the six different species analysed in detail also indicate high variability in the identified variables and their respective effect sizes for the two cities and the two study seasons. Gehrt and Chelsvig (2004), in a similar study in the Chicago area, also identified a great variability in urban bat species that favour certain habitat types. Altogether, our findings support the results of Scanlon and Petit (2008b) who concluded from their echolocation study of urban bats in Adelaide parklands that large sample sizes, possibly selected on long time periods, are needed for the identification of clear habitat selection patterns because of the large variation in call activity.

5.5.1 Conclusions

This study has shown that spatial information explains significant portions of total variation in bat occurrence and activity. Spatial MEM variables identify important patterns in these socially organised species. The distribution of roosts in space critically determines the bats’ occurrences when hunting in urban areas. To our knowledge, this study is the first to use these advanced spatial techniques to relate this crucial ecological information to any socially organised (colonial) species. We found a high variability in the selection of different foraging habitats measured on different radii in all species under scope. The foraging niche of urban bats best explains this pattern. All six species regularly occurring in cities are aerial hawkers that prey opportunistically on the most abundant flying insects. In urban areas, insect biomass may change rapidly due to climatic conditions (wind, temperature) and a presumed high degree of stochasticity in occurrence. Two out of the six regularly found urban bat species (*P. kuhlii, H. savii*) have invaded cities north of the alpine arch only in last two decades. This remarkable and fast range expansion exemplifies that cities, due to their warmer climate, offer special and new habitat conditions that are continuously explored by species. When found to be suitable, the colonisers will promptly exploit the newly found niches. In this way, cities potentially anticipate changes in fauna that will also happen in other environments under continuing global warming.

Acknowledgements

We thank the house owners that provided access to their properties and the authorities of Lucerne, Lugano and Zurich for their support of the project. We are grateful to the following people for support in field work or statistical matters: J. Ambrosini, D. Borcard, B. Krummenacher, S. Fontana, R. Home, D. Kouakou, P. Legendre, F. Maurer, S. von Felten. R. Home and U. Kormann improved earlier versions of the manuscript. Special thanks go to M. Lehmann.

GIS layers were obtained from the Swiss Federal Office of Topography (Vector25 © 2009 swisstopo, DV033594). This study forms part of the interdisciplinary project 'BiodiverCity' (www.biodivercity.ch) which aims at the identification, maintenance and enhancement of biodiversity and their acceptance in the urban development process. BiodiverCity was funded by the Swiss National Science Foundation as a project of NRP54 'Sustainable development of the built environment' (www.nrp54.ch).

5.6 References

Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 68:460-471.

Artuso, R., S. Bovet, and A. Streilein. 2003. Practical methods for the verification of countrywide terrain and surface models. International Archives for Photogrammetry, Remote Sensing and Spatial Information Sciences 34:6.

Avila-Flores, R. and M. B. Fenton. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. Journal of Mammalogy 86:1193-1204.

Bates, D., M. Maechler, and B. Dai. 2008. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-18.

Blake, D., A. M. Hutson, P. A. Racey, J. Rydell, and J. R. Speakman. 1994. Use of Lamplit Roads by Foraging Bats in Southern England. Journal of Zoology 234:453-462.

Bontadina, F., S. F. Schmied, A. Beck, and R. Arlettaz. 2008. Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat. Journal of Applied Ecology 45:641-648.

Bontadina, F., H. Schofield, and B. Naef-Daenzer. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. Journal of Zoology 258:281-290.

Borcard, D. and P. Legendre. 1994. Environmental control and spatial structure in ecological communities: an example using Oribatid mites (Acari, Oribatei). Environmental and Ecological Statistics 1:37-61.

Borcard, D. and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51-68.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826-1832.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73:1045-1055.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a practical information-theoretic approach. Springer-Verlag, New York.

Dietz, C., O. Von Helversen, and D. Nill. 2007. Handbuch der Fledermäuse Europas und Nordwestafrikas. Biologie, Kennzeichen, Gefährdung. Kosmos, Stuttgart.

Dietz, M., J. A. Encarnacao, and E. K. V. Kalko. 2006. Small scale distribution patterns of female and male Daubenton's bats (*Myotis daubentonii*). Acta Chiropterologica 8:403-415.

Dray, S. 2008. SpacemakeR: Spatial modelling.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483-493.

Duelli, P., M. K. Obrist, and D. R. Schmatz. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture Ecosystems & Environment 74:33-64.

Fontana, S., T. Sattler, F. Bontadina, and M. Moretti. submitted. How to manage the urban green to enhance bird species richness and diversity. Biological Conservation.

Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. Biological Conservation 126:528-539.

Fortin, D. and M. R. T. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press.

Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology-Revue Canadienne De Zoologie 65.

Gaisler, J., J. Zukal, Z. Rehak, and M. Homolka. 1998. Habitat preference and flight activity of bats in a city. Journal of Zoology 244:439-445.

Gehrt, S. D. and J. E. Chelsvig. 2003. Bat activity in an urban landscape: Patterns at the landscape and microhabitat scale. Ecological Applications 13:939-950.

Gehrt, S. D. and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. Ecological Applications 14:625-635.

Germann, C., T. Sattler, M. K. Obrist, and M. Moretti. 2008. Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 81 141-154.

Giannini, N. P., and E. K. V. Kalko. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105:209-220.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. G. Wu, X. M. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. Science 319:756-760.

Grindal, S. D. and R. M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. Ecoscience 6:25-34.

Haffner, M. and H. P. Stutz. 1985/86. Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at street-lamps. Myotis 23-24:167-172.

Hourigan, C. L., C. P. Catterall, D. Jones, and M. Rhodes. 2008. A comparison of the effectiveness of bat detectors and harp traps for surveying bats in an urban landscape. Wildlife Research 35:768-774.

Ineichen, S., and M. Ruckstuhl. in press. Stadtfauna. Grün Stadt Zürich. Haupt Verlag, Bern.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101–108.

Klausnitzer, B. 1988. Verstädterung von Tieren. A.Ziemsen Verlag, Wittenberg Lutherstadt.

Kunz, T. H. and M. B. Fenton. 2003. Bat Ecology. University of Chicago Press, Chicago.

Kurta, A. and J. A. Teramino. 1992. Bat Community Structure in an Urban Park. Ecography 15:257-261.

Legendre, P. and L. Legendre. 1998. Numerical ecology. 2nd edition. Elsevier Science PV, Amsterdam.

Legendre, P., X. C. Mi, H. B. Ren, K. P. Ma, M. J. Yu, I. F. Sun, and F. L. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Lesinski, G., E. Fuszara, and M. Kowalski. 2000. Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes. Zeitschrift Fur Saugetierkunde-International Journal of Mammalian Biology 65:129-137.

Likens, G. 1991. Human-accelerated environmental change. Bioscience 41:130.

Liu, J., G. C. Daily, P. R. Ehrlich, and G. W. Luck. 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421:530-533.

Marzluff, J. M. 2001. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston.

McDonnell, M. J., J. Breuste, and A. K. Hahs. 2009. Introduction: Scope of the book and need for developing a comparative approach to the ecological study of cities and towns. Pages 1-5 in M. J. McDonnell, A. K. Hahs, and J. Breuste, editors. Ecology of Cities and Towns. A comparative Approach. Cambridge University Press.

Neuweiler, G. 1989. Foraging Ecology and Audition in Echolocating Bats. Trends in Ecology & Evolution 4:160-166.

Nicholls, B. and P. A. Racey. 2006. Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. Behavioral Ecology and Sociobiology 61:131-142.

Obrist, M. K., R. Boesch, P. F. Flückiger, and U. Dieckmann. 2004a. Who's calling? Acoustic bat species identification revised with synergetics. Pages 484-492 in T. e. al., editor. Advances in the study of echolocation in bats and dolphins. Proceedings of the Biosonar Conference 1998. University of Chicago Press, Chicago.

Obrist, M. K., P. F. Flückiger, and R. Boesch. 2004b. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. Mammalia 69:307-322.

Obrist, M. K., E. Rathey, P. Christe, F. Bontadina, A. Martinoli, M. Condedera, and M. Moretti. in review. Response of bat species composition to change in chestnut orchard management. Biological Conservation.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, M. H. H. Stevens, and H. H. Wagner. 2008. vegan: Community Ecology Package.

Parris, K. M. and D. L. Hazell. 2005. Biotic effects of climate change in urban environments: The case of the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne, Australia. Biological Conservation 124:267-276.

Parsons, S., and M. K. Obrist. 2004. Recent methodological advances in the recording and analysis of chiropteran biosonar signals in the field. Proceedings of the Biosonar Conference 1998. Pages 468-477 in: Advances in the study of echolocation in bats and dolphins. University of Chicago Press, Chicago.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87:2614-2625.

Pinto, N. and T. H. Keitt. 2008. Scale-dependent responses to forest cover displayed by frugivore bats. Oikos 117:1725-1731.

Popa-Lisseanu, A. G., F. Bontadina, and C. Ibanez. 2009. Giant noctule bats face conflicting constraints between roosting and foraging in a fragmented and heterogeneous landscape. Journal of Zoology 278:126-133.

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhodes, M. and C. Carferall. 2008. Spatial foraging behavior and use of an urban landscape by a fast-flying bat, the molossid *Tadarida australis*. Journal of Mammalogy 89:34-42.

Russo, D. and G. Jones. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. Journal of Zoology 258:91-103.

Rydell, J. 1992. Exploitation of Insects around Streetlamps by Bats in Sweden. Functional Ecology 6:744-750.

Sattler, T., F. Bontadina, A. H. Hirzel, and R. Arlettaz. 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. Journal of Applied Ecology 44:1188-1199.

Sattler, T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M. K. Obrist, and M. Moretti. in preparation. Human impact prevents spatial processes in arthropod and bird communities in urban ecosystems.

Sattler, T., P. Duelli, M. K. Obrist, R. Arlettaz, and M. Moretti. submitted. Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecology.

Scanlon, A. T. and S. Petit. 2008a. Biomass and biodiversity of nocturnal aerial insects in an Adelaide City park and implications for bats (Microchiroptera). Urban Ecosystems 11:91–106.

Scanlon, A. T. and S. Petit. 2008b. Effects of site, time, weather and light on urban bat activity and richness: considerations for survey effort. Wildlife Research 35:821-834.

Siemers, B. M. and H.-U. Schnitzler. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429:657-661.

Smith, R. M., P. H. Warren, K. Thompson, and K. J. Gaston. 2006. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15:2415-2438.

Sukopp, H., H.-P. Blume, and W. Kunick. 1979. The soil, flora and vegetation of Berlin’s wastelands. Pages 115-132 in I. C. Laurie, editor. Nature in Cities. John Wiley, Chichester.

Sukopp, H. and R. Wittig. 1998. Stadtökologie. 2nd edition. Fischer, Stuttgart

Thompson, K., J. G. Hodgson, R. M. Smith, P. H. Warren, and K. J. Gaston. 2004. Urban domestic gardens (III): Composition and diversity of lawn floras. Journal of Vegetation Science 15:373-378.

Vaughan, N., G. Jones and S. Harris. 1997a. Habitat use by bats (Chiroptera) assessed by means of a broad- band acoustic method. Journal of Applied Ecology 34:716-730.

Vaughan, N., G. Jones and S. Harris. 1997b. Identification of British bat species by multivariate analysis of echolocation call parameters. Bioacoustics 7:189-207.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494-499.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Zingg, P. E. 1990. Akustische Artidentifikation von Fledermäusen (Mammalia: Chiroptera) in der Schweiz – Acoustic Species Identification of Bats (Mammalia, Chiroptera) in Switzerland. Revue Suisse de Zoologie 97:263-294.

Zipperer, W. C., J. G. Wu, R. V. Pouyat, and S. T. A. Pickett. 2000. The application of ecological principles to urban and urbanizing landscapes. Ecological Applications 10:685-688.

5.7 Tables and figures

Table 1: Environmental variables used in the analysis. Variables are listed according to the four data sets 'local', 'R50m', 'R250m', 'R1000m', which correspond to spatial extent of measurements (measured locally at the sampling point and on the three radius 50m, 250m, 1000m radius around the sampling points; for further details see Methods).

Name	Explanation	Units
Local variables		
Elevation	Meter above sea level	m
Slope		%
Eastness	Exposition with respect to East	Gradient from -1 to 1
Northness	Exposition with respect to North	Gradient from -1 to 1
Distance to water [3]	Minimal euclidean distance to the nearest large water body (river, lake)	km
Land cover map in radius 50m, 250m, 1000m (linear and quadratic terms)		
Buildings[1,3]	Area covered by Buildings	km^2
Roads[1,3]	Area sealed by roads	km^2
Urban Green[1,3]	Area of Urban Green	km^2
Woody plants[2,3]	Area of trees and bushes	km^2

[1] Obtained from theme specific layer of the topographic map 1:25000 of Switzerland

[2] Obtained from Digital Surface Model

[3] Linear and quadratic term used

Table 2: Minutes with bat activity for the six (Lucerne) and five species (Zurich) which yielded sufficient numbers for statistical analysis and the corresponding numbers for the three call type groups.

Species	**Lucerne**	**Zurich**
Hypsugo savii	94	65
Nyctalus noctula	83	40
Pipistrellus kuhlii	216	247
Pipistrellus nathusii	641	433
Pipistrellus pipistrellus	1259	533
Pipistrellus pygmaeus	310	1*
Call type groups		
FM – FC call types > 32 kHz[1]	2175	1320
FM – FC call types < 32 kHz[2]	174	45*
FM call types[3]	51*	13*

* not analysed

[1] Genus Pipistrellus and Hypsugo

[2] Genus Eptesicus, Vespertilio and Nyctalus

[3] Genus Myotis, Plecotus

Table 3: AICc-selected environmental variables and corresponding effect sizes (± SE) according to species or call type groups, A) Lucerne, B) Zurich. Elevation in meters, slope in %, exposition (eastness, northness) in a gradient from -1 to 1, distances in km and land cover variables in km^2. Repro: reproduction season, Post-repro: Post-reproduction season.

A: Lucerne	*Hypsugo savii*		*Nyctalus noctula*		*Pipistrellus kuhlii*		*Pipistrellus nathusii*		*Pipistrellus pipistrellus*		*Pipistrellus pygmaeus*		FM-FC > 32kHz		FM-FC < 32kHz	
	Repro	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**
Local variables																
Elevation																
Slope		-0.2 ±0.0								0.0 ±0.1	0.1 ±0.0			0.0 ±0.1		
Eastness		1.5 ±0.1				0.8 ±0.3		0.6 ±0.5					0.3 ±1.2		-0.5 ± 0.2	
Northness				-0.9 ±0.1					-0.5 ±0.5		-0.8 ±0.1					-0.4 ± 0.3
Dist. to water	-6.8 ±3.3		-5.4 ±1.1		-6.8 ±3.3		-6.8 ±3.3				4.1 ±1.3	0.9 ±2.1			-4.6 ± 1.2	
Dist. to water2	2.3 ±3.7		2.1 ±0.9		2.3 ±3.7		2.3 ±3.7				-4.8 ±1.1	-2.2 ±1.6			2.3 ± 0.9	
Land cover variables R50m																
Buildings		9.6 ±3.0			2.1 ±6.1		26.0 ±7.9		38.2 ±37.8		84.5 ±11.0	-0.4 ±4.9				
Roads							-33.0 ±15.0				-25.8 ±10.1				-13.9 ± 6.3	
Urban Green							1.6 ±8.9		-21.8 ±43.9		-72.2 ±13.7	10.3 ±6.3				
Woody plants		-88.5 ±4.6			-43.6 ±14.8	-31.2 ±13.7	3.6 ±24.9		19.3 ±45.0							
Buildings2		3.0 ±4.2			6.5 ±11.2		-30.8 ±17.4		-72.2 ±93.2		-185.3 ±30.2	-17.7 ±12.2				
Roads2							134.2 ±77.5				60.1 ±52.7				81.1 ± 24.3	
Urban Green2							-15.4 ±9.3		26.2 ±43.7		85.0 ±13.3	-4.9 ±6.2				

Woody plants2	283.0 ±13.7		143.5 ±43.3	112.0 ±40.2	38.8 ±76.9		-40.5 ±138.3							
Land cover variables R250m														
Buildings	-0.8 ±0.2					0.5 ±0.7		0.8 ±1.5					0.51 ± 0.35	
Roads	0.6 ±0.7		-1.8 ±1.6			0.0 ±2.4					-0.1 ±5.9		-0.18 ± 0.84	
Urban Green	-1.1 ±0.2				-3.4 ±1.2							-0.9 ±2.0		
Woody plants	-1.3 ±0.2				1.7 ±0.9		0.7 ±1.5		3.3 ±0.5					
Buildings2	0.1 ±0.0					0.0 ±0.1		-0.1 ±0.1					-0.09 ± 0.04	
Roads2	0.1 ±0.1		0.4 ±0.2			0.1 ±0.4					0.1 ±0.9		0.12 ± 0.11	
Urban Green2					0.2 ±0.1							0.0 ±0.1		
Woody plants2	0.1 ±0.0				-0.2 ±0.1		-0.1 ±0.2		-0.3 ±0.0					
Land cover variables R1000m														
Buildings	-0.1 ±0.0				0.2 ±0.1	0.1 ±0.1							0.12 ± 0.04	
Roads			-0.3 ±0.2				-0.3 ±0.4				-0.2 ±0.5		-0.27 ± 0.09	-0.19 ± 0.13
Urban Green					-0.3 ±0.1				0.1 ±0.1					
Woody plants									0.2 ±0.1					
Buildings2													-0.001 ± 0.0004	
Roads2													0.005 ± 0.001	0.004 ± 0.002

Urban Green2								
Woody plants2								

B: Zurich	*Hypsugo savii*		*Nyctalus noctula*		*Pipistrellus kuhlii*		*Pipistrellus nathusii*		*Pipistrellus pipistrellus*		*Pipistrellus pygmaeus*	FM-FC > 32kHz		FM-FC < 32kHz	
	Repro	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	**Repro**	**Post-repro**	Not analysed	**Repro**	**Post-repro**	**Repro**	**Post-repro**
Local variables															
Elevation	No variables selected													No variables selected	
Slope															
Eastness			-0.8 ± 0.2										-0.6 ±0.7		
Northness					0.8 ±0.3				-0.5 ±0.4	-0.5 ±0.3					
Dist. to water				-0.9 ±1.3											
Dist. to water2				-0.5 ±0.8											
Land cover variables R50m															
Buildings															
Roads			1729 ± 332												
Urban Green			6400 ± 110												
Woody plants															
Buildings2															
Roads2			-201600 ± 119700												

Urban Green2		-746100 ± 11850						
Woody plants2								
Land cover variables R250m								
Buildings								
Roads		245.4 ± 60.2						
Urban Green								
Woody plants					45.8 ±127.6			
Buildings2								
Roads2		-2821 ± 1068						
Urban Green2								
Woody plants2					-121.8 ±1261.0			
Land cover variables R1000m								
Buildings								
Roads		13.8 ± 9.0		50.3 ±21.4 34.8 ±15.6	52.0 ±31.2		54.1 ±41.3 22.1 ±40.1	
Urban Green					24.2 ±14.5			
Woody plants				-16.3 ±10.5 -20.6 ±7.4			-19.9 ±19.7 -13.9 ±19.2	
Buildings2								
Roads2		-7.0 ± 10.8		-61.6 ±26.9 -37.2 ±19.4	-67.8 ±40.7		-66.1 ±53.1 -23.3 ±51.1	
Urban Green2					-7.6 ±4.4			
Woody plants2				7.9 ±6.6 12.0 ±4.6			11.9 ±12.1 8.2 ±11.8	

Table 4: Results of variation partitioning in Lucerne (A) and in Zurich (B); italics and bright grey = 5-10%, italics and dark grey = >10%.

A) Lucerne		*H. savii*	*N. noctula*	*P. pipistrellus*	*P. nathusii*	*P. kuhlii*	*P. pygmaeus*	FM-FC > 32kHz	FM-FC < 32kHz	Average
Reproduction period	Environ-mental	0.7%	13.4%	21.2%	28.8%	7.6%	30.4%	8.8%	20.1%	16.4%
	Food	0.5%	0.0%	4.5%	0.1%	0.0%	10.3%	0.0%	0.0%	1.9%
	Spatial	4.4%	4.5%	0.3%	0.8%	0.0%	0.0%	1.5%	0.0%	1.4%
	Env & Food	0.5%	0.0%	0.0%	0.1%	2.5%	0.0%	1.7%	2.3%	0.9%
	Food & Spatial	1.0%	0.4%	0.0%	0.0%	0.1%	0.3%	0.0%	0.0%	0.2%
	Env & Spatial	6.0%	8.0%	6.4%	1.3%	8.6%	1.4%	8.6%	18.2%	7.3%
	Env & Food & Spatial	0.6%	0.0%	0.0%	0.7%	1.1%	0.0%	1.0%	0.0%	0.4%
	Total Explained	**13.5%**	**26.3%**	**32.5%**	**31.7%**	**19.8%**	**42.4%**	**21.6%**	**41.4%**	**28.7%**
Post-Reproduction Period	Environ-mental	10.0%	5.8%	2.9%	14.2%	19.2%	5.1%	12.9%	2.5%	9.1%
	Food	0.0%	0.9%	0.0%	8.5%	0.0%	0.0%	0.0%	0.6%	1.3%
	Spatial	0.0%	13.4%	0.0%	0.4%	8.9%	2.4%	2.6%	6.0%	4.2%
	Env & Food	0.0%	1.3%	1.0%	0.0%	1.1%	1.0%	0.0%	0.9%	0.7%
	Food & Spatial	0.1%	0.0%	0.0%	1.1%	0.0%	0.4%	0.0%	2.1%	0.5%
	Env & Spatial	11.6%	0.6%	0.8%	18.7%	3.6%	10.6%	0.0%	15.7%	7.7%
	Env & Food & Spatial	3.1%	0.0%	0.3%	0.0%	0.0%	0.5%	0.9%	0.0%	0.6%
	Total Explained	**24.9%**	**22.0%**	**5.1%**	**42.9%**	**32.8%**	**19.9%**	**16.4%**	**27.7%**	**24.0%**

B) Zurich		*H. savii*	*N. noctula*	*P. pipistrellus*	*P. nathusii*	*P. kuhlii*	*P. pygmaeus*	FM-FC > 32kHz	FM-FC < 32kHz	Average
Reproduction period	Environ-mental	ns	3.4%	2.5%	4.3%	3.4%	Due to low numbre not analysed	8.3%	ns	4%
	Food	2.0%	1.3%	0.0%	0.0%	1.3%		0.0%		1%
	Spatial	7.0%	22.2%	11.5%	9.1%	22.2%		12.5%	ns	14%
	Env & Food	ns	0.0%	0.6%	2.4%	0.0%		0.1%	ns	1%
	Food & Spatial	0.0%	4.3%	0.0%	0.0%	4.3%		0.3%	ns	1%
	Env & Spatial	ns	4.3%	8.3%	14.3%	4.3%		22.6%	ns	11%
	Env & Food & Spatial	ns	0.0%	4.7%	0.0%	0.0%		0.0%	ns	1%
	Total Explained	**9.0%**	**35.5%**	**27.5%**	**30.1%**	**35.5%**		**43.8%**	**ns**	**30%**
Post-Reproduction Period	Environ-mental	ns	6.6%	0.6%	6.8%	ns		9.2%	ns	6%
	Food	1.5%	0.4%	1.0%	0.0%	0.0%		0.0%		0%
	Spatial	0.9%	1.1%	8.0%	2.1%	4.6%		0.2%	ns	3%
	Env & Food	ns	0.0%	0.2%	0.0%	ns		1.3%	ns	0%
	Food & Spatial	0.0%	1.0%	0.0%	0.4%	0.0%		0.0%	ns	0%
	Env & Spatial	ns	0.0%	15.5%	15.1%	ns		7.8%	ns	10%
	Env & Food & Spatial	ns	0.0%	0.0%	0.0%	ns		0.0%	ns	0%
	Total Explained	**2.4%**	**9.2%**	**25.2%**	**24.5%**	**4.6%**		**18.4%**	**ns**	**14%**

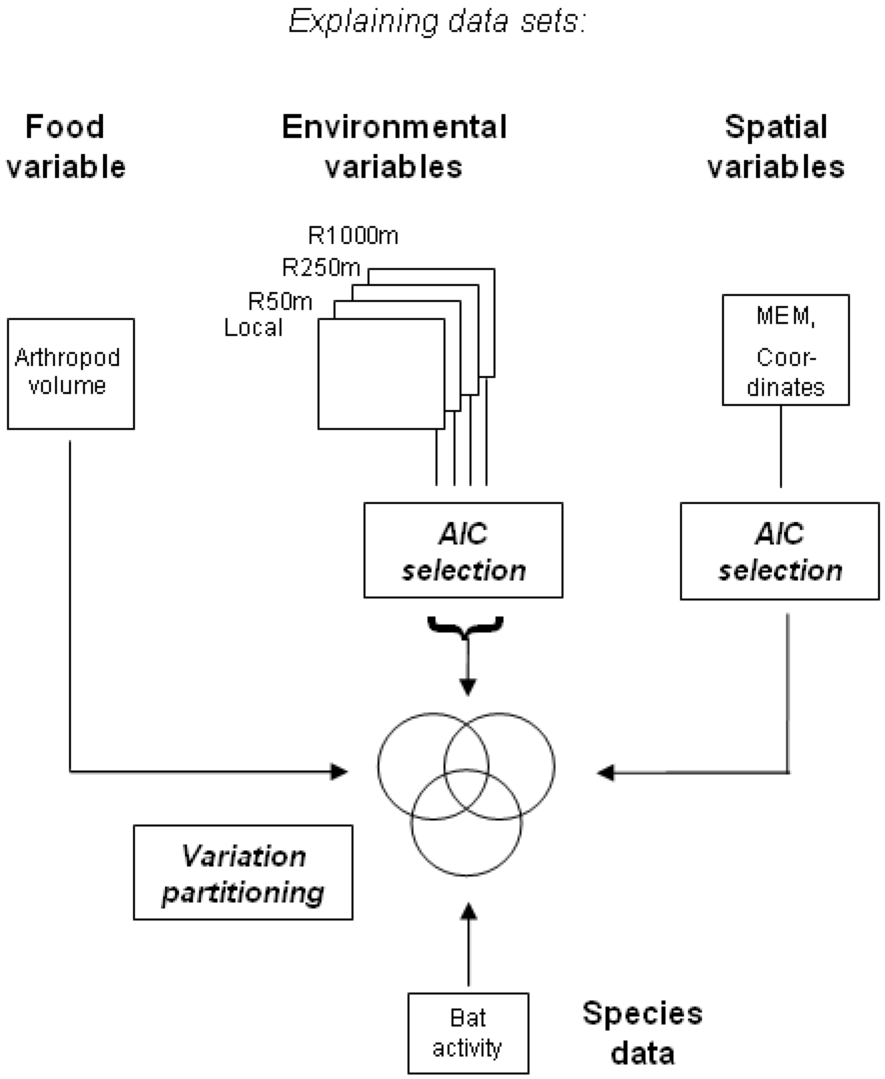

Fig. 1: The analytical steps with the three explaining data sets used that were repeated for each species and species group in both, the reproduction and the post-reproduction period and for Lucerne and Zurich individually.

5.8 Supplementary material

Table S1: Overview on the generalised linear mixed-effects models formulated a-priori which were evaluated for bat activity of all species analysed (individually per city and period). For the local data set 32 models were formulated (A), while for each of the three data sets for radius 50m, 250m and 100m 16 models were formulated and consequently selected with AICc procedures (B). All models shown also included the two co-variables time after sunset and temperature (not shown) which are known to affect bat activity. Distance to water was modeled as linear and quadratic term. See Table 1 for variable definition. As bat activity was measured twice per period, bat activity is aggregated within random factor 'sampling location' (explicit model formulation not shown).

A)

0 *(Null-model)*
1 Elevation
2 Slope
3 Eastness
4 Northness
5 Distance to water
6 Elevation+Slope
7 Elevation+Eastness
8 Elevation+Northness
9 Elevation+Distance to water
10 Slope+Eastness
11 Slope+Northness
12 Slope+Distance to water
13 Eastness+Northness
14 Eastness+Distance to water
15 Northness+Distance to water
16 Elevation+Slope+Eastness
17 Elevation+Slope+Northness
18 Elevation+Slope+Distance to water
19 Elevation+Eastness+Northness
20 Elevation+Eastness+Distance to water
21 Elevation+Northness+Distance to water
22 Slope+Eastness+Northness
23 Slope+Eastness+Distance to water
24 Slope+Northness+Distance to water
25 Eastness+Northness+Distance to water
26 Elevation+Slope+Eastness+Northness
27 Elevation+Slope+Eastness+Distance to water

28	Elevation+Slope+Northness+Distance to water
29	Elevation+Eastness+Northness+Distance to water
30	Slope+Eastness+Northness+Distance to water
31	Elevation+Slope+Eastness+Northness+Distance to water

B)

Model -Nr.	**Candidate Models**
0	*(Null-model)*
1	Building+Building2
2	Sealed+Sealed2
3	Urban+Urban2
4	TreeBush+TreeBush2
5	Building+Sealed+Building2+Sealed2
6	Building+Urban+Building2+Urban2
7	Building+TreeBush+Building2+TreeBush2
8	Sealed+Urban+Sealed2+Urban2
9	Sealed+TreeBush+Sealed2+TreeBush2
10	Urban+TreeBush+Urban2+TreeBush2
11	Building+Sealed+Urban+Building2+Sealed2+Urban2
12	Building+Sealed+TreeBush+Building2+Sealed2+TreeBush2
13	Building+Urban+TreeBush+Building2+Urban2+TreeBush2
14	Sealed+Urban+TreeBush+Sealed2+Urban2+TreeBush2
15	Building+Sealed+Urban+TreeBush+Building2+Sealed2+Urban2+TreeBush2

Table S2: Summary of bat activity in Lucerne. Activity for the species included (total number of minutes with activity for all four replicates of 45 minutes recording time (total 180 minutes) per sampling location).

Sampling location	*Hypsugo savii*	*Nyctalus noctula*	*Pipistrellus kuhlii*	*Pipistrellus nathusii*	*Pipistrellus pipistrellus*	*Pipistrellus pygmaeus*
201	3	1	27	28	41	
202	1	1		13	55	
203		1	1		18	1
204		1		7	72	2
205			3	3	32	5
206		2	3	10	104	30
207	2	2	6	7	26	9
208	1	4	14	38	80	38
209	3	1	11	25	12	1
210	13		13	73	16	3
211	28	1	32	43	11	
212	3	2	5	16	30	2
213		3	4	36	44	
214	19	11	10	20	38	
215	16	16	30	113	103	38
216	2	2	4	35	26	12
217		1	5	14	33	18
218		5	4	18	65	33
219		1	8	6	13	11
220			2	17	52	3
221		3	4	19	22	6
222		3	3	2	44	3
223			2	1	26	1
224		8		2	26	7
225				7	49	16
226		1		4	32	5
227	1	1	2	4	16	11
228			4	20	33	3
229	1	2	6	11	29	21
230		1		4	60	2
231		5	7	43	37	23
232	1	4	6	2	14	6
Total	**94**	**83**	**216**	**641**	**1259**	**310**

Table S3: Summary of bat activity in Zurich. Activity for the species included (total number of minutes with activity for all four replicates of 45 minutes recording time (total 180 minutes) per sampling location).

Sampling location	*Hypsugo savii*	*Nyctalus noctula*	*Pipistrellus kuhlii*	*Pipistrellus nathusii*	*Pipistrellus pipistrellus*
101	4	1	31	34	8
102	4	1	4	10	9
103			3	9	12
104	6		15	24	8
105	1	1	1	3	15
106		1	3	5	3
107			5	22	13
108	1		4	15	8
109	13	1	18	25	22
110			6	4	8
111			1	5	11
112		5		4	10
113		1	2		
114	1		28	24	21
115		1	2	4	14
116			2	2	5
117	2		27	43	45
118	1	5	4	28	1
119		3	2	13	14
120	1	2	3	6	57
121	3	1	9	18	18
122	8		2	7	59
123			7	7	35
124	1	4	10	12	17
125	1	2	2	4	11
126	12	1		5	26
127	1	1	12	6	16
128		2		15	9
129			1	5	8
130	1	1	6	4	4
131	1	4	33	60	24
132	3	2	4	10	22
Total	**65**	**40**	**247**	**433**	**533**

6

Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea)

Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea)

Christoph Germann[1], Thomas Sattler[2, 3], Martin K. Obrist[4], Marco Moretti[2]

[1] Mittlere Strasse 14, CH-3600 Thun, Switzerland

[2] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[3] Zoological Institute, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland

[4] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

Published in *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 81:141-154.

6.1 Abstract

The phytophagous group of weevils (Curculionoidea) was sampled in the three Swiss cities of Lucerne, Lugano and Zurich. In total, 3448 individuals from 129 species were collected (Lucerne: 64 species; Lugano: 69 species; Zurich: 83 species). The most dominant species were the xero-thermophilous *Protapion trifolii* and the ubiquist *Tychius picirostris*. Most of the 13 dominant and subdominant species found in three cities live on Fabaceae. Species similarity (Soerensen index) was highest between the cities of Lucerne and Zurich, which could be expected since they belong to the same biogeographical region (Midlands). The occurrences of five weevil species that are worthy of note with regard to the Swiss fauna are discussed in detail. For two of the species – *Ceutorhynchus leprieuri* and *Hypophyes pallidulus* – their capture in Switzerland is only the 2nd confirmed occurrence since they were first reported 87 and 170 years ago respectively. The sampling of the blind edaphic *Ferreria marqueti* in urban environments in Lucerne and Zurich confirm that individuals captured in Switzerland are displaced specimens. A further six species were recorded for the first time in the two biogeographical regions of the Midlands and Southern Switzerland. A complete species list is presented.

Keywords

Switzerland, biodiversity, urban environment, urban habitat, faunistics

6.2 Introduction

The urban environment is one of the most steadily increasing habitats in Switzerland and in the World (Schuler et al. 2004, United Nations 2000). Urban areas increased in Switzerland by 327 km^2 between 1982 and 1995, and the urbanisation process is continuing. The built area in Switzerland comprises 2’800 km^2 (7% of the total surface) and in the Swiss Midlands region, the built area has reached 1’620 km^2 (15%), (Bundesamt für Raumentwicklung 2005, Bundesamt für Statistik 2005). It is therefore important to include urban areas when undertaking faunistical surveys so that a complete picture of the diversity and distribution of the taxonomic group under consideration is obtained.

Weevils sensu lato (Curculionoidea) represent one of the most species rich Coleopteran groups in Switzerland with more than 1050 species. Many new findings, as well as changes in systematics and taxonomy, have added to the diversity of this important group in Switzerland (Germann 2006b) since the publication of the last comprehensive lists from Stierlin & Gautard (1867) and Stierlin (1898). Until very recently, new weevil records from urban environments in Switzerland have remained scarce and accidental. However, no less than 7 weevil species (Germann 2004, 2005, 2006a, 2006b, 2006c, 2007) that are new to the Swiss fauna have been recorded exclusively from urban environments since 2004.

Weevils were included in the first comprehensive work on urban habitats and their fauna in middle Europe (Klausnitzer 1988). An analysis of species composition, based on plentiful data collected by Cholewicka (1981) in the city of Warsaw, provided first insights into the urban weevil fauna and showed both a strongly decreasing number of species and an increasing proportion of grassland species towards the city centre. Most recent studies in urban Central Europe either deal with single weevil species (e.g. Bayer 2001, *Ceutorhynchus canaliculatus*; Sprick et al. 2002, *Rhopalapion longirostre*; Germann et al. 2005b, *Otiorhynchus crataegi* and *Pachyrhinus lethierryi*), cover only a small amount of total weevil diversity (Kaupp et al. 2004, 19 species found on vegetated roofs in Basel; Flechtner & Klinger

1991, 15 species found in Frankfurt/Main; Kadas 2006, 13 species found on green roofs in London), or present results of accidental captures (Gosik 2007, weevils found on sticky traps in Lublin). Recently, a study of insect-diversity was done in the zoo of Basel, where weevils were represented by 41 species (Sprecher et al. 2008).

This paper fills a gap in the knowledge of the weevil fauna in urban environments in Switzerland, where current data is almost lacking. We give a short overview of dominance, structure, and frequency of urban weevils in the three Swiss cities Lucerne, Lugano, and Zurich. The data presented includes new species occurrences for bio-geographical regions of Switzerland. We discuss the most interesting findings with respect to the Swiss fauna and present a complete species list in Supplementary material. This contribution forms part of the BiodiverCity project (www.biodivercity.ch; Moretti 2005) that aims to assess biodiversity in urban environments and its acceptance by citizens in the framework of the national research programme "Sustainable development of the built environment" (www.nfp54.ch).

6.3 Materials and methods

The study took place in three Swiss cities, namely Lucerne, Lugano, and Zurich (Table 1, Figs. 1-3) in 2006. A total of 106 sampling locations were chosen, with 34 locations in Lucerne and 36 each in Lugano and Zurich. In each city, 32 locations were chosen to cover the widest variability possible along the three gradients “age of green area”, “sealed area” (in a radius of 25 m around trap), and “human management” (measured by the amount of meadow mowing within 5 m of the trap). The remaining 2 sampling locations in Lucerne and the 4 in Lugano and Zurich were selected in ruderal areas.

Weevils were sampled using standard sampling methods (Duelli et al. 1999). Litter dwelling species were sampled using pitfall traps, which consisted of 3 plastic beakers recessed into the soil (opening diameter 75 mm; arranged in an isosceles triangle with a distance of one meter).

Transparent roofs installed approximately 8 cm above the beakers provided protection from the rain. Flying and flower visiting species were sampled using so called combination traps, i.e. non-directional window traps in combination with a yellow water pan placed at a height of 1.5 m above ground. Both, pitfall and combination traps, were filled with the same 0.2% Metatin (bactericide) solution. One trap set, consisting of three beakers and one combination trap, was installed at each of the 106 locations. The minimum distance between two locations, and between each individual location and the town margin was at least 250 m. The sampling period was in accordance with the Rapid Biodiversity Assessment, for which the seven weeks with the presence of most insect species had been determined (Duelli & Obrist 2005). Traps were opened in week 23 (between June 13th and 15th) and then emptied weekly during seven weeks until week 31 (closure between August 1st and 3rd).

Soerensen index and Dominance indices (DI) are calculated after Mühlenberg (1989) and classification of the different dominance levels follows the logarithmic scale proposed by Engelmann (1978), with the modification that the eudominance level is not indicated here (i.e. dominant > 10%; subdominant 3.2-10%; minor species < 3.2%).

The frequency (F) expresses the fraction of sample locations per city where the species was found (100% = 36 locations in Zürich and Lugano; 100% = 34 locations in Lucerne).

The first author identified the weevil species. Nomenclature follows the propositions in the catalogue by Alonso-Zarazaga & Lyal (1999, 2002) in respect of the genus-level, and details concerning the species level are taken from Alonso-Zarazaga (2007). The species occurrence in Switzerland is shown according to the six different Swiss biogeographic regions as defined by Gonseth et al. (2001). Specimens of the five species that are exceptional for the Swiss fauna are deposited in the Nature-Museum Lucerne.

6.4 Results and discussion

A total of 3448 individuals representing 129 species were found (Lucerne: 64 species /min 1, max 15 per sample location/, 841 individuals; Lugano: 69 species /min 1, max 11/, 840 individuals; Zurich: 83 species /min 2, max 16/, 1767 individuals). Overall, 22.5% (29 species) of the species were found in all three cities, 20.9% (27 species) in two of them, and 56.6% (71 species) were exclusively found in one city (Supplementary material Appendix S1). In the course of this study, six weevil species were found in a biogeographical region where they had not been found previously. In the Midlands (North of the Alps) one, and in the Southern Alps (canton of Ticino) five, species were found for the first time (Table 2).

We experienced some trap failures due to storms or to intentional damage to elements of some trap sets. However, for the purpose of this study, the samples of single locations of each city were pooled and have been analysed on city level. The losses of individuals on city level are estimated to sum up to 0.7% for Lucerne, 3.9% for Lugano and 1.6% for Zurich. Based on the asymptotic relationship between individuals and species, the number of species missed per city by these losses is a fraction of these percentages and in all cases less than 0.5 %. Therefore we consider the losses negligible and we have continued to use the original data for the analysis.

Although the number of species found per city is comparable to other studies in urban habitats, direct comparison with other studies is difficult because the sampling period was short (7 weeks) in this study and/or other sampling methods were applied in potentially comparable studies. In contrast to the standardized sampling scheme implemented in our study, experienced specialists often collect weevils actively, which can reveal many species within a short time. While acknowledging difficulties in comparison caused by different sampling efforts and different sampling sizes, species numbers in other cities start at 31 (Lau 1975, zoological garden Berlin) and 41 (Sprecher et al. 2008, zoological garden Basel) and peak at 193 (parks of Warsaw, but only 33 species in the city centre), and 210 in Lublin

(Klausnitzer 1988, overview of both cities). However, intensive sampling of Curculionoidea in urban habitats (including adjacent areas) may result in many more species as shown for Berlin with 521 species (Winkelmann 1991) or for the small Swiss Canton of Geneva (which is dominated by urban area), where 661 species were registered (Germann, unpublished).

The comparison of the weevil species composition between the three cities based on the Soerensen index revealed that Lucerne and Zurich, which are both located in the biogeographical region Midlands, showed the highest similarity (these cities share 60.3% of the species found in both cities), whereas lower similarity values were found for the comparison between Lugano (biogeographical region Southern Alps) and the two Midlands cities (Lugano-Lucerne: 50.0%; Lugano-Zurich: 49.4%). These differences are consistent with our expectations, since the particular insubric climate (i.e. wet, warm summers and mild, dry winters) and the proximity of the Mediterranean region affect the species composition of Lugano and the Alps hinder faunal exchange.

The species dominance rank distribution indicates that the weevil community in all three cities is mostly dominated by a single species (*Protapion trifolii*), which accounts for 25% or more of all individuals found (Lucerne: 25%; Lugano: 44%; Zurich: 30%). *Tychius picirostris* is dominant in Zurich (13%) and subdominant in Lucerne (8%) and Lugano (6%). Other subdominant species included *Barypeithes pellucidus* (Lucerne 7%; Zurich 3%) and *Otiorhynchus porcatus* (Lucerne 3%; Zurich 4%), although both species were absent in Lugano, as well as *Tychius pusillus* (Zurich 3.5%, but which was scarce in Lucerne and Lugano). Dominant and subdominant species are marked in bold in the species list (Supplementary material Appendix S1).

The dominance of *Protapion trifolii*, the occurrences of *Tychius pusillus* and *Squamapion flavimanum* in all three cities, and the occurrence of *Trichosirocalus rufulus* in Zurich (5 individuals) were unexpected, since all four species were considered to be restricted to natural habitats such as calcareous grasslands (Mesobromion and Xerobromion) in Switzerland. An explanation for the occurrence of these xero-thermophilous and rarely found species (with the exception of the common *P. trifolii*) could be that the climate in urban habitats is comparatively warm and dry. These findings are consistent with the results of other studies that comprise various beetle taxa (e.g. Kaupp et al. 2004) and with the general idea that the urban microclimatic condition favours species relying on higher ambient temperatures (Cholewicka 1981).

The occurrences of the remaining dominant and subdominant species are consistent with our expectations as they are common species associated to grassland habitats, especially to the wide spread grassland-type Arrhenaterion (Germann et al. 2005a) or polyphagous ubiquists such as *Otiorhynchus porcatus* or *Barypeithes pellucidus*. The findings of the polyphagous *B. pellucidus* in Lucerne and Zurich support the strong affinity of this species to urban environments, as mentioned in Klausnitzer (1988), and is further supported by new data from Basel (Sprecher et al. 2008). In the latter study, the species was eudominant and represented more than 50% of the individuals from among the 41 species sampled.

The ten most common species sampled in the three cities live on host plants belonging to the Fabaceae, with the exception of the two polyphagous species (*Otiorhynchus porcatus* and *Barypeithes pellucidus*) and *Anthonomus rubi* that live on Rosaceae. The dominance of Fabaceae-related species living in the urban environment is consistent with those that occur in the natural- and seminatural (agricultural) environments.

The frequency distribution of the species sampled was calculated to obtain a value describing the regularity of the species' occurrences within each city (Supplementary material Appendix S1). All seven species that were found at F ≥50% were either subdominant or dominant species. The most dominant species *Protapion trifolii* was found with high frequency (F ≥ 70.6%) in all three cities. The three subdominant species Barypeithes pellucidus, Otiorhynchus porcatus and Tychius meliloti show lower frequency values (F = 8.8%-44.4%). We suspect the preference for shaded and more humid conditions by *O. porcatus* explains its irregular occurrence, as this habitat type is found uncommonly in the urban environment. The irregular occurrence of *T. meliloti* might be explained by its patchily distributed host plant *Melilotus sp.*, which mostly grows on ruderal sites.

We now give detailed information on the findings of five selected species in alphabetical order. Three of them were found in a biogeographical region for the first time, one was found only for the second time and in an area of a region where it had not been recorded previously (*Otiorhynchus pinastri*) and one is discussed because of the ongoing debate about its origin (*Ferreria marqueti*):

Ceutorhynchus leprieuri Brisout, 1881

The reported finding of this species in the Canton of Ticino by Künnemann (1920) was the first and only record in Switzerland. The two specimens found in this study represent the first recorded findings in the biogeographic region Midlands, which confirms the occurrence of this species in Switzerland 86 years after its first observation. Due to its widespread distribution in surrounding Europe, the occurrence of *Ceutorhynchus leprieuri* in the Midlands has been expected for quite some time.

Ferreria marqueti (Aubé, 1863)

Ferreria marqueti is a blind edaphic species of mainly Mediterranean origin which was reported in Switzerland by Fontana (1947) near to Chiasso in the Canton of Ticino and Besuchet (1964) in the Lac Léman region (Western Switzerland). In February 2007, a single male of *F. marqueti* was found in Basel (Rheinhalde) in Northern Switzerland. Two additional specimens were then found in the Basel Zoo (Sprecher et al. 2008). In the present study, two individuals were found in Lucerne and one in Zurich. Following the Rheinhalde finding in 2007, the media speculated that *F. marqueti* could have survived the ice ages in the ice free zone of Basel and thus represent a relic species from the tertiary period (Basler Zeitung: 7th and 16th of March 2007, Neue Zürcher Zeitung: 7th of March 2007, Tages-Anzeiger: 7 th of March 2007 and critical remarks by Jedicke (2007a, b)). This speculation is contradicted by the occurrence of *F. marqueti* in Lucerne and Zurich, which were both covered by ice during the ice age. A more likely explanation is that F. marqueti has been introduced to the study region by human activity.

Owen (1997) suspected transport within soil or among roots of garden shrubs as the reason for the presence of this species in England. This hypothesis is supported in that specimen were found in gardens within cities where plants and soil have been continuously imported by human activity. We agree with Sprecher et al. (2008) that the relic hypothesis should definitely be considered as very unlikely.

Hypophyes pallidulus (Gravenhorst, 1807)

Hypophyes pallidulus had only been previously found in the Valais (Southwestern Switzerland) by Stierlin & Gautard (1867), Favre (1890) and Stierlin (1898). However, these reports are unconvincing as the main distribution of this species lays in the Mediterranean. More recently, three specimens of *H. pallidulus* were rediscovered in the Natural History Museum of Geneva (2 ex. Geneva, coll. Tournier. 1 ex. Valais, coll. Melly) by Germann (unpublished data). All the specimens are from the ancient collection (before 1900) and therefore the indications on the labels are doubtful since inaccurate labelling has been reported for other taxa (e.g. Marggi 1992; Carabidae). Hoffmann (1958) states that *H. pallidulus* lives on *Tamarix africana* Webb. and *T. gallica* L. (Tamaricaceae), neither of which occur naturally in Switzerland.

The finding of three specimens of *Hypophyes pallidulus* in Lugano, 170 years after the first doubtful record, confirms the occurrence of the species in Switzerland. Furthermore, this is the first reported finding in Southern Switzerland. However, the existence of a viable population of *H. pallidulus* still remains questionable due to the absence of the host plant (*Tamarix* spp.). The findings in Geneva and Valais point to the possibility that *H. pallidulus* may also accept *Myricaria germanica* (L.) Desv. as a host plant, as *Myricaria germanica* is the only Tamaricaceae species occurring in the area. A further possibility is that *H. pallidulus* might live on *Tamarix* spp., which are cultivated in gardens as ornamental plants. Both hypotheses need further investigation.

Otiorhynchus pinastri (Herbst, 1795)

The species, found in a single specimen in Zurich, is a neobiont in Switzerland. It originates in Eastern Europe and individuals have been captured in Switzerland since 1979 (Germann 2004). Until this finding in Zurich, it had been found only in the Canton of Bern (Germann 2006b).

Sitophilus zeamais Motschulsky, 1855

A review of the collections in the Natural History Museum of Bern produced the following detections, as an amendment to the specimens presented by Germann (2007: 182): 2 ex. Bern, Biel, 1.1916, leg. A. Mathey. 1 ex. Basel, 25.5.1974, leg. F. Straub. 11 ex. Bern, Stadt Bern, 12.4.1985. 1 ex. Ticino, Arzo, "par battage", 30.6.1988, leg. P. Scherler. 1 ex. Ticino, Somazzo, 27.6.1990, leg. P. Scherler, 6 ex. Bern, Orpund, "in Reis aus Thailand", 20.12.2001, leg. R. Naef.

These 22 specimens from Midlands and Southern Switzerland show that *S. zeamais* has been present in Switzerland since 1916. In this study we recorded the species in Lugano which provides further evidence of this species in Southern Switzerland and adds to the previously reported Swiss records from Geneva and Basel (Germann 2007). This synanthropic and cosmopolitan species species is a pest in crop products and its presence in Switzerland is not surprising as corn and rice has been traded worldwide for a long time.

6.5 Conclusions

This study provides the first discussion of the weevil fauna in urban habitats in Switzerland. Altogether, 129 weevil species were found in Lucerne, Lugano, and Zurich. Despite the short sampling period (seven weeks in June and July), the results show that weevil species richness in the three Swiss cities is rather high, peculiar, and dominated by a xero-thermophilous species (*Protapion trifolii*) that is likely to find suitable habitats due to the warm and dry conditions in the urban environment. The rediscovery of two species (*Ceutorhynchus leprieuri* and *Hypophyes pallidulus*) in Switzerland after 87 and 170 years respectively, indicates that the urban environment hosts a unique species composition. This particular species composition appears to be the result of two distinct phenomena. Firstly, the dense mosaic of different habitats and warm-dry climatic conditions within cities provides a habitat in which highly specialised species as well as neobionts can survive. Secondly, individual colonists are introduced involuntarily with the transport of soils and plants, which is evidenced by the presence of the blind edaphic *Ferreria marqueti* in cities north of the Alps.

Acknowledgements

The authors would like to thank the house owners that provided access to their properties and the authorities of Lucerne, Lugano and Zurich for their support of the project. We are grateful to Vanessa Albin, Raphaël Arlettaz, Fabio Bontadina, Peter Duelli, Franco Fibbioli, Robert Home, Wolfgang Kastenholz, Maria Kindermann, Arlette Niederer, Alexandra Schulz, Regula Siegwart and Peter Wirz who helped in the field, in the lab or in organizing the project.

The project was funded by the Swiss National Science Foundation in the framework of the National Research Program NRP54 "Sustainable development of the built environment" (www.nfp54.ch).

6.6 References

Alonso-Zarazaga, M. A. 2007. Curculionoidea in: Fauna Europaea Version 1.3 (19. April 2007). – URL: http://www.faunaeur.org

Alonso-Zarazaga, M.A. & Lyal, C.H.C. 1999. A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera). (Excepting Scolytidae and Platypodidae). – Entomopraxis, Barcelona, 315 pp.

Alonso-Zarazaga, M.A. & Lyal, C.H.C. 2002. Addenda and corrigenda to 'A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera)'. – Zootaxa 63: 1-37.Bayer, Ch. 2001. Zur Biologie, Verbreitung und Populationsdynamik von *Ceutorhynchus canaliculatus* im Berliner Stadtgebiet. – Snudebiller 2: 41–50.

Besuchet, C. 1964. Coléoptères endogés des environs de Genève. – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 36 (4): 312–320.

Bundesamt für Raumplanung (Herausgeber). 2005. Raumentwicklungsbericht 2005.

Eidgenössisches Departement für Umwelt, Verkehr, Energie und Kommunikation (UVEK), Bern. 116 pp.

Bundesamt für Statistik (Herausgeber). 2005. Arealstatistik Schweiz: Zahlen – Fakten – Analysen, Neuchâtel. 99 pp.

Cholewicka, K. 1981. Curculionids (Coleoptera, Curculionidae) of Warsaw and Mazovia. – Memorabilia Zoologica 34: 235-258.

Duelli, P. & Obrist, M. K. 2005. Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). – Schriftenreihe der Forschungsanstalt Reckenholz 56: 132–38.

Duelli, P., Obrist, M. K. & Schmatz, D. R. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. – Agriculture Ecosystems & Environment 74 (1-3): 33–64.

Engelmann, H. D. 1978. Zur Dominanzklassifizierung von Bodenarthropoden. – Pedobiologia 18: 378–380.

Favre, E. 1890. Faune des Coléoptères du Valais et des régions limitrophes. – Nouvelles Mémoires de la Société Helvetique des Sciences Naturelles 31. 448 pp.

Flechtner, G., Klinger, R. 1991. Zur Insektenfauna einer Großstadt: Käferfunde aus Frankfurt/Main. – Mitteilungen des internationalen entomologischen Vereins 16 (1/2): 37–82.

Fontana, P. 1947. Contribuzione alla Fauna coleotterologica ticinese. – Bolletino della Società Ticinese di Scienzia Naturale 42: 16–93.

Germann, Ch. 2004. *Otiorhynchus pinastri* (Herbst, 1795) – ein invasiver Xenobiont aus dem östlichen Europa in der Schweiz (Coleoptera, Curculionidae). – Mitteilungen der Entomologischen Gesellschaft Basel 54 (3/4): 110–114.

Germann, Ch. 2005. *Pachyrhinus lethierryi* (Desbrochers, 1875) signalé pour la première fois en Suisse (Coleoptera, Curculionidae: Polydrusini). – Bulletin Romand d`Entomologie 23: 57–59.

Germann, Ch., Schmidt, M., Frank, T. & Bacher, S. 2005a. Beetles and calcareous grassland conservation: how specific are leaf beetles, weevils and ground beetles? Master thesis. Philosophisch-naturwissenschaftliche Fakultät der Universität Bern. 25 pp.

Germann, Ch., Bahr, F., Bayer, C., Behne, L., Müller, G. & U., Sprick, P., Stüben, P. & Winkelmann, H. 2005b. First record of *Pachyrhinus lethierryi* (Desbrochers, 1875) and *Otiorhynchus crataegi* Germar, 1824 at the Niederrhein (Germany: Rhineland) (Curculionidae: Entiminae: Polydrusini). – Weevil News 28: 1–3. URL: http://www.curci.de/Inhalt.html

Germann, Ch. 2006a. *Otiorhynchus armatus* Boheman, 1843 – eine weitere Art für die Schweizer Fauna aus dem Tessin (Coleoptera, Curculionidae). – Mitteilungen der Entomologischen Gesellschaft Basel 56 (3): 91–94.

Germann, Ch. 2006b. Beitrag zur Rüsselkäfer-Fauna der Schweiz – mit der Meldung von 17 weiteren Arten (Coleoptera, Curculionoidea). – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 79: 299–309.

Germann, Ch. 2006c. *Otiorhynchus smreczynskii* Cmoluch, 1968 – nun auch in der Schweiz (Coleoptera, Curculionidae, Entiminae). – Mitteilungen der Entomologischen Gesellschaft Basel 56 (4): 122–126.

Germann, Ch. 2007. Zweiter Beitrag zur Rüsselkäfer-Fauna der Schweiz – mit der Meldung von 23 weiteren Arten (Coleoptera, Curculionoidea). – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 80: 167–184.

Gonseth, Y., Wohlgemuth, T., Sansonnens, B., Buttler, A. 2001. Die biogeographischen Regionen der Schweiz. – Schriftenreihe Natur und Landschaft Nr. 137. Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern.

Gosik, R. 2007. Weevils (Coleoptera: Curculionoidea) from sticky traps against the horse-chestnut leafminer Cameraria ohridella Deschka & Dimic. – ChronÏmy Przyrode Ojczysta 63 (5): 3–18.

Hoffmann, A. 1958. Faune de France No. 62. Coléoptères Curculionides 3ième partie. – Editions Paul Lechevalier, Paris: 1210–1839.

Jedicke, E. 2007a. Aktuelles. Käferfund in Basel. – Naturschutz und Landschaftsplanung 39 (4): 106.

Jedicke, E. 2007b. Ein Käfer als Ente – Naturschutz und Landschaftsplanung 6: 162.

Kaupp, A., Brenneisen, S., Klausnitzer, B. & Nagel, P. 2004. Eco-faunistic characteristics of the beetle fauna of vegetated roofs (Insecta: Coleoptera). – Entomologische Blätter für Biologie und Systematik der Käfer 100 (1): 47-83

Kadas, G. 2006. Rare invertebrates colonizing green roofs in London. – Urban Habitats 4 (1): 66-86. URL: http://www.urbanhabitats.org

Klausnitzer, B. 1987. Verstädterung von Tieren. 2. Auflage (1988) – Ziemsen-Verlag, Wittenberg. 316 pp.

Künnemann, G. 1920. Die mitteleuropäischen Ceutorrhynchus-Arten aus der Gruppe des chalybaeus Germar (Coleoptera). – Entomologische Mitteilungen IX (7/9): 124–130.

Lau, D. 1975. Zur Käferfauna im Tierpark Berlin 1. Milu, Leipzig 3: 690-709.

Marggi, W. 1992. Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Coleoptera Teil 1/Text, Teil 2/Verbreitungskarten. Dokumenta Faunistica 13: 477 + 243 pp.

Moretti, M. 2005. Verbessern Tiere und Pflanzen die Lebensqualität der Stadt? In: Glogger, B., Jud, A., Mehl, A. (eds.) Nachhaltige Siedlungs- und Infrastrukturenentwicklung – NFP54. Schweizerischer Nationalfonds, Bern. 34 pp.

Mühlenberg, M. 1989. Freilandökologie, 2nd edition. UTB für Wissenschaft/Uni Taschenbücher. – Quelle & Meyer Verlag, Heidelberg. 432 pp.

Owen, J. A. 1997. Observations on Raymondionymus marqueti (Aubé) (Col. Curculionidae) in north Surrey. – The Entomologist 116 (2): 122–129.

Schuler, M., Perlik, M. & Pasche, N. 2004. Nicht-städtisch, rural oder peripher – wo steht der ländliche Raum heute? – ARE, Bundesamt für Raumentwicklung, Bern.125 Seiten.

Sprecher, E., Luka, H., Germann, Ch., Luka, A., Klausnitzer, B. & Graff, P. 2008. Kapitel 19, Käfer. In: Baur, B., Billen, W. & Burckhardt, D. (Redaktion). Vielfalt zwischen den Gehegen: wildlebende Tiere und Pflanzen im Zoo Basel – Monographien der Entomologischen Gesellschaft Basel 3: 308-331.

Sprick, P., H. Winkelmann & L. Behne 2002. *Rhopalapion longirostre* – Anmerkungen zur Biologie und aktuellen Ausbreitung in Deutschland. – Weevil News 8: 1–9. URL: http://www.curci.de/Inhalt.html

Stierlin, G. 1898. Fauna Coleopterorum Helvetica. Teil II. – Bolli und Boecherer, Schaffhausen. 662 pp.

Stierlin, G. & Gautard, V.V. 1867. Fauna coleopterorum helvetica, die Käfer-Fauna der Schweiz. – Schaffhausen und Vevey. 354 pp.

United Nations. 2000. Urban Agglomerations. 1999. United Nations, New York.

Winkelmann, H. 1991. Liste der Rüsselkäfer (Coleoptera: Curculionidae) von Berlin mit Angaben zur Gefährdungssituation ("Rote Liste"). In: Auhagen, A. Platen, R. & Sukopp, H. (Hrsg.) 1991. Rote Listen der gefährdeten Pflanzen und Tiere in Berlin. – Landschaftsentwicklung und Umweltforschung 6: 319–357.

6.7 Tables and figures

Table 1: Location and size of the three cities investigated in the framework of the project BiodiverCity: Lucerne, Lugano and Zurich.

Cities investigated (number of trap sites)	**Lucerne** (n = 34)	**Lugano** (n = 36)	**Zurich** (n = 36)
Canton	Lucerne	Ticino	Zurich
Biogeographical region	Midlands	Southern Alps	Midlands
Geographical Coordinates	47°03’N 8°18’E	46°00’N 8°57’E	47°22’N 8°33’E
Area	24 km²	26 km²	92 km²
Elevation a.s.l.	436 m	273 m	408 m
Inhabitants (December 2005)	57’533	49'223	366’809

Table 2: The following 6 species of Curculionoidea were recorded for the first time for the respective biogeographical region in Switzerland during the project BiodiverCity. The numbers below the biogeographical regions are the number of specimens sampled (listed in alphabetical order).

Family/genus/species	**Biogeographical region**	
	Midlands	**Southern Switzerland**
Curculionidae		
Ceutorhynchus leprieuri C. Brisout, 1881	2	
Magdalis memnonia (Gyllenhal, 1837)		1
Magdalis rufa (Germar, 1824)		2
Xylosandrus germanus (Blandford, 1894)		1
Dryophthoridae		
Sitophilus zeamais Motschulsky, 1855		1
Nanophyidae		
Hypophyes pallidulus (Gravenhorst, 1807)		3

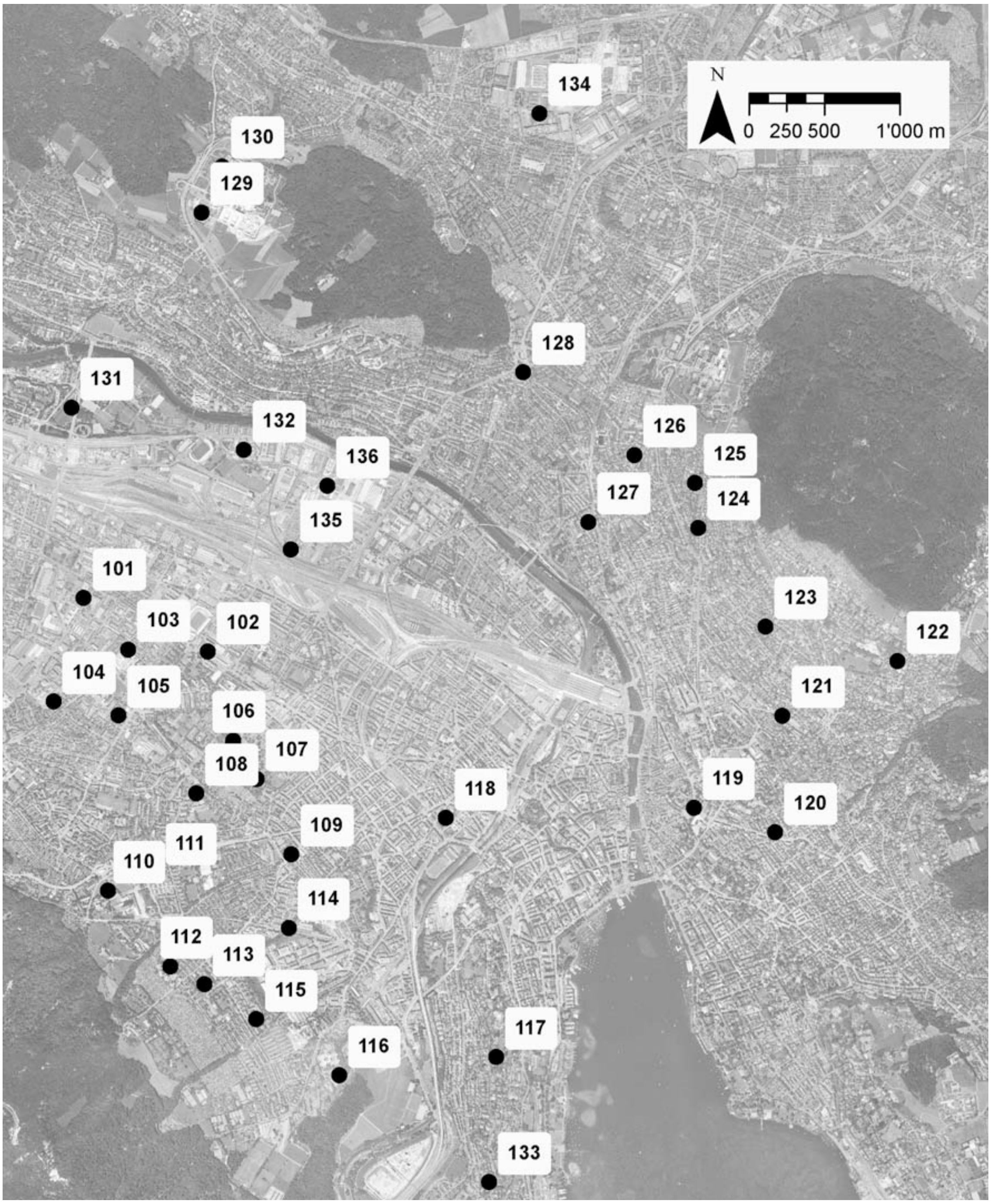

Fig. 1: Sampling locations in the city of Zurich (n=36). Swissimage © 2008 swisstopo (DV033492).

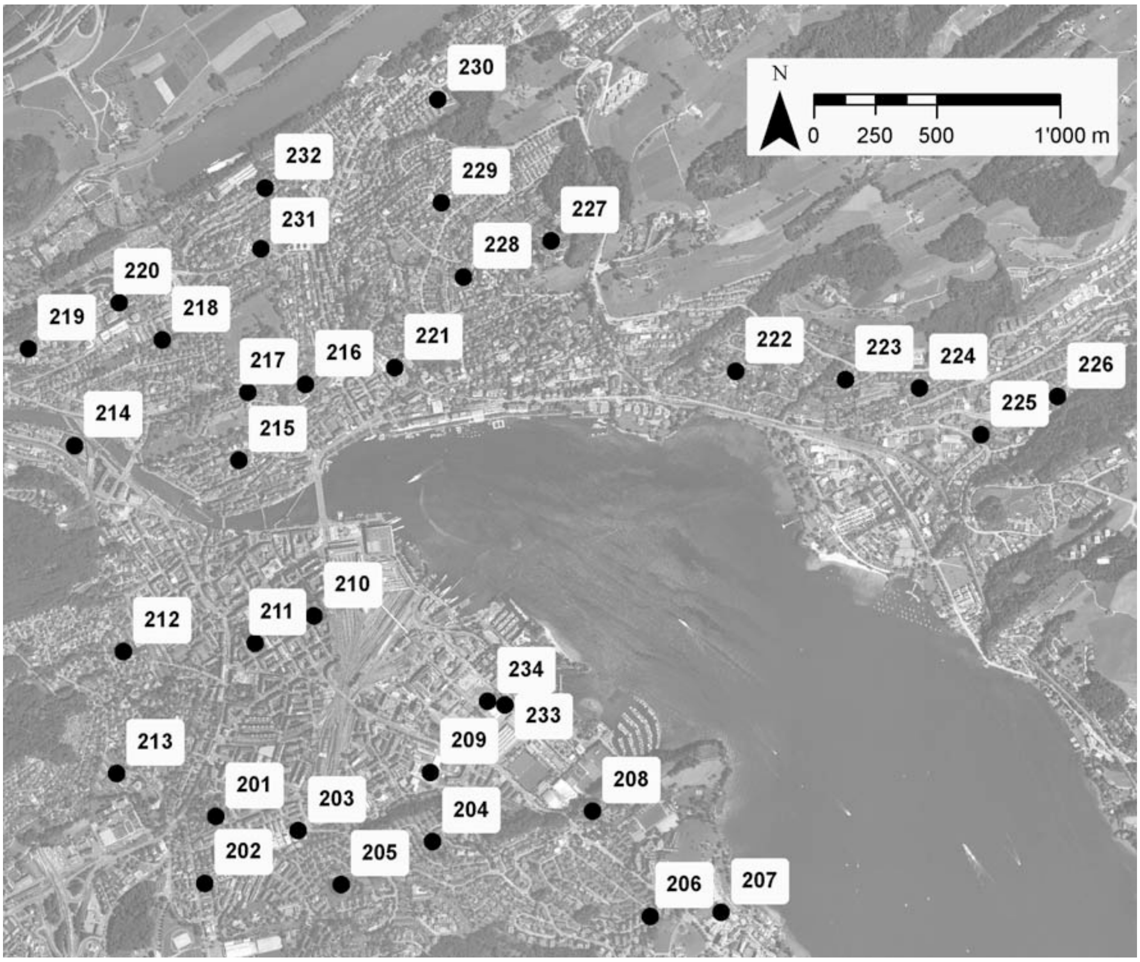

Fig. 2: Sampling locations in the city of Lucerne (n=34). Swissimage © 2008 swisstopo (DV033492).

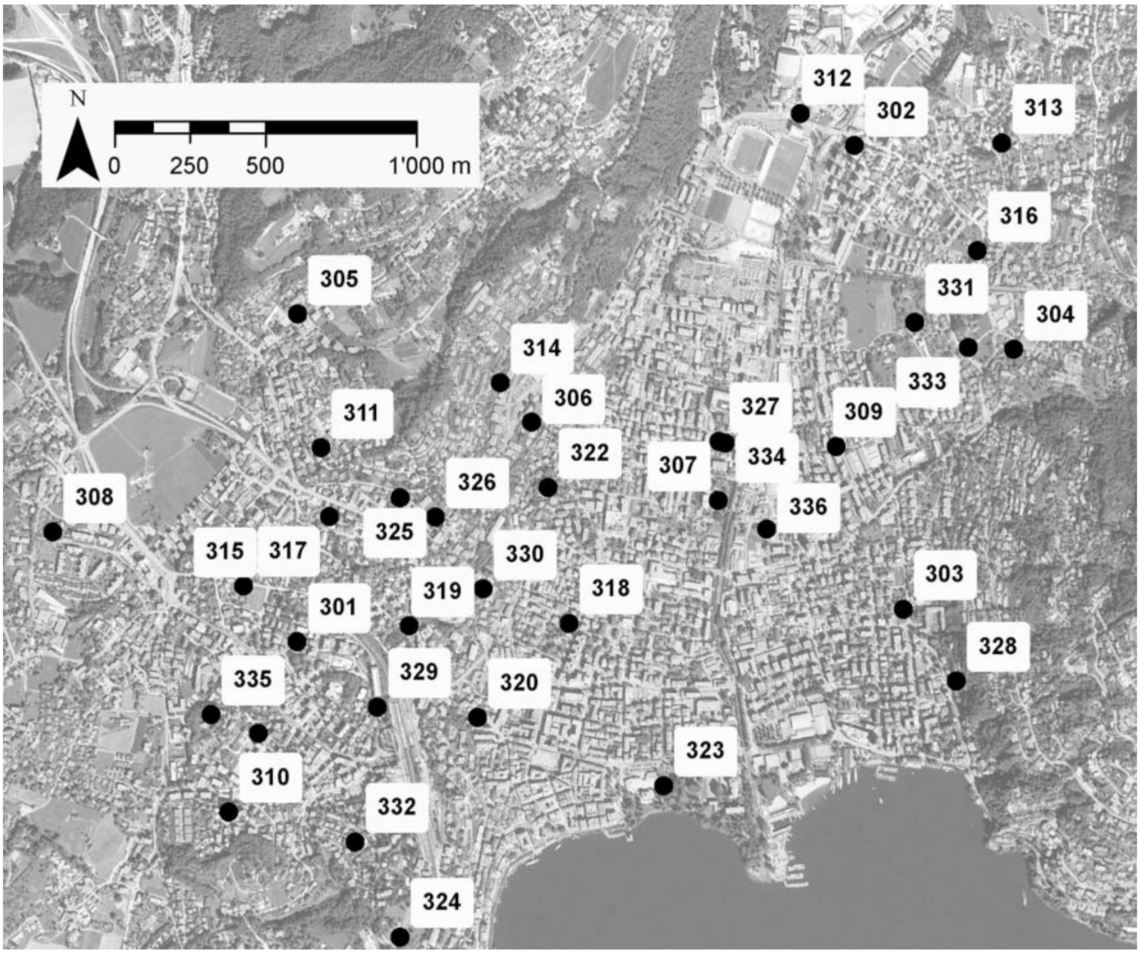

Fig. 3: Sampling locations in the city of Lugano (n=36). Swissimage © 2008 swisstopo (DV033492).

6.8 Supplementary material

Appendix S1: Number of individuals of the 129 Curculionoidea species (in alphabetical order) sampled in the cities of Lucerne, Lugano and Zurich from 12th of June to 3rd of August 2006 in pitfall- and combination traps (see Methods). Species numbers are marked as follows: dominant species (> 10%) are in bold with an asterisk, subdominant species (3.2-10%) are in bold. The frequency (F, see methods for calculation) is indicated in % on the right side in each column, values of 50% or more are in bold. Nomenclature by the catalogue of Alonso-Zarazaga & Lyal (1999, 2002), details on the species-level by Alonso-Zarazaga (2007).

Genus/species	**Cities**						**Total**
	Lucerne	F (%)	Lugano	F (%)	Zurich	F (%)	
Anthribidae							
Bruchela rufipes (Olivier, 1790)					1	2.8	1
Apionidae							
Aspidapion radiolus (Marsham, 1802)	2	5.9					2
Betulapion simile (Kirby, 1811)	5	11.8	21	30.6	5	11.1	31
Catapion meieri (Desbrochers, 1901)					1	2.8	1
Catapion pubescens (Kirby, 1811)			2	2.8	2	5.6	4
Catapion seniculus (Kirby, 1808)	5	5.9	16	19.4	24	27.8	45
Ceratapion onopordi (Kirby, 1808)			1	2.8			1
Diplapion stolidum (Germar, 1817)			6	11.1			6
Eutrichapion ervi (Kirby, 1808)	1	2.9					1
Eutrichapion punctigerum (Paykull, 1792)	1	2.9			3	5.6	4
Eutrichapion vorax (Herbst, 1797)					1	2.8	1
Ischnopterapion loti (Kirby, 1808)					3	2.8	3
Ischnopterapion modestum (Germar, 1817)			1	2.8			1
Ischnopterapion virens (Herbst, 1797)	19	23.5	10	19.4	**87**	38.9	116
Malvapion malvae (Fabricius, 1775)	2	5.9	1	2.8	3	8.3	6
Oxystoma ochropus (Germar, 1818)					1	2.8	1
Protapion apricans (Herbst, 1797)	**36**	38.2	15	25	**137**	41.7	188
Protapion assimile (Kirby, 1808)	**30**	26.5	5	8.3	48	33.3	83
Protapion fulvipes (Fourcroy, 1785)	**38**	47.1	**26**	36.1	52	**61.1**	116
Protapion nigritarse (Kirby, 1808)			3	2.8	2	5.6	5
Protapion ononidis (Gyllenhal, 1827)			6	5.6			6
Protapion trifolii (Linné, 1768)	*** 104**	**70.6**	*** 117**	**75**	*** 536**	**83.3**	757
Protapion varipes (Germar, 1817)			1	2.8			1
Pseudapion moschatae (Hoffmann, 1938)					3	8.3	3

Pseudapion rufirostre (Fabricius, 1775)			1	2.8	1	2.8	2
Rhopalapion longirostre (Olivier, 1807)			1	2.8			1
Squamapion flavimanum (Gyllenhal, 1833)	6	5.9	1	2.8	11	16.7	18
Stenopterapion tenue (Kirby, 1808)					1	2.8	1
Taeniapion urticarium (Herbst, 1784)			1	2.8			1
Attelabidae							
Attelabus nitens (Scopoli, 1763)	1	2.9	1	2.8			2
Curculionidae							
Anthonomus rubi (Herbst, 1795)	**41**	**50**	4	11.1	26	41.7	71
Archarius pyrrhoceras (Marsham, 1802)	2	5.9	1	2.8			3
Aulacobaris lepidii (Germar, 1824)	13	17.6			8	16.7	21
Aulacobaris picicornis (Marsham, 1802)					1	2.8	1
Bagous tempestivus (Herbst, 1795)	1	2.9					1
Barynotus moerens (Fabricius, 1792)	2	5.9					2
Barynotus obscurus (Fabricius, 1775)					1	2.8	1
Barypeithes araneiformis (Schrank, 1781)	2	5.9					2
Barypeithes pellucidus pellucidus (Boheman, 1843)	**55**	35.3			**60**	36.1	115
Barypeithes trichopterus (Gautier, 1863)	11	5.9			1	2.8	12
Ceutorhynchus leprieuri Brisout, 1881					2	2.8	2
Ceutorhynchus obstrictus (Marsham, 1802)	3	8.8	14	30.6	14	27.8	31
Ceutorhynchus pallidactylus (Marsham, 1802)					4	11.1	4
Ceutorhynchus typhae (Herbst, 1795)	5	14.7	7	19.4	10	22.2	22
Curculio nucum Linné, 1758	5	14.7	1	2.8	5	13.9	11
Donus zoilus (Scopoli, 1763)			1	2.8			1
Glocianus distinctus (C. Brisout, 1870)	4	11.8			4	8.3	8
Glocianus punctiger (Gyllenhal, 1837)					5	8.3	5
Graptus triguttatus triguttatus (Fabricius, 1775)	1	2.9					1
Gymnetron veronicae (Germar, 1821)	1	2.9					1
Hylesinus toranio (Danthoine, 1788)			1	2.8			1
Hylurgops palliatus (Gyllenhal, 1813)					1	2.8	1
Hypera meles (Fabricius, 1792)					2	5.6	2
Hypera nigrirostris (Fabricius, 1775)	1	2.9	2	5.6	12	11.1	15
Hypera postica (Gyllenhal, 1813)	1	2.9	1	2.8			2
Larinus obtusus Gyllenhal, 1836					2	2.8	2
Leiosoma deflexum (Panzer,	5	8.8			5	5.6	10

1795)							
Liophloeus tessulatus (Müller, 1776)	1	2.9			2	5.6	3
Magdalis memnonia (Gyllenhal, 1837)			1	2.8			1
Magdalis rufa (Germar, 1824)			1	2.8	1	2.8	2
Mecinus circulatus (Marsham, 1802)			5	13.9			5
Mecinus pascuorum (Gyllenhal, 1813)			3	8.3			3
Mecinus pyraster (Herbst, 1795)	1	2.9	5	11.1	3	5.6	9
Mononychus punctumalbum (Herbst, 1784)	2	5.9			5	13.9	7
Orchestes fagi (Linné, 1758)	2	5.9					2
Orchestes testaceus (Müller, 1776)					1	2.8	1
Orthochaetes setiger (Beck, 1817)			1	2.8			1
Otiorhynchus crataegi Germar, 1824	1	2.9			3	8.3	4
Otiorhynchus frescati Boheman, 1843			6	11.1			6
Otiorhynchus ligneus (Olivier, 1807)					1	2.8	1
Otiorhynchus ovatus (Linné, 1758)			8	19.4	2	5.6	10
Otiorhynchus pinastri (Herbst, 1795)					1	2.8	1
Otiorhynchus porcatus (Herbst, 1795)	22	32.4			**66**	44.4	88
Otiorhynchus pupillatus Gyllenhal, 1834	3	2.9					3
Otiorhynchus raucus (Fabricius, 1777)	1	2.9					1
Otiorhynchus rugosostriatus (Goeze, 1777)	2	5.9			4	8.3	6
Otiorhynchus salicicola Heyden, 1908	1	2.9	1	2.8			2
Otiorhynchus singularis (Linné, 1767)					1	2.8	1
Otiorhynchus sulcatus (Fabricius, 1775)	3	2.9	1	2.8	5	2.8	9
Otiorhynchus uncinatus Germar, 1824	1	2.9					1
Otiorhynchus veterator Uyttenboogaart, 1932	1	2.9					1
Phyllobius betulinus (Bechstein & Scharfenberg, 1805)					1	2.8	1
Phyllobius maculicornis Germar, 1824					1	2.8	1
Phyllobius oblongus (Linné, 1758)					3	5.6	3
Phyllobius roboretanus Gredler, 1882					1	2.8	1
Polydrusus cervinus (Linné, 1758)			1	2.8			1
Polydrusus formosus (Mayer, 1779)	2	5.9			7	13.9	9
Polydrusus impressifrons Gyllenhal, 1834					1	2.8	1
Polydrusus pterygomalis Boheman, 1840	5	11.8					5
Rhinoncus bruchoides (Herbst,	5	8.8			4	11.1	9

1784)							
Rhinoncus pericarpius (Linné, 1758)	6	11.8	1	2.8	1	2.8	8
Rhinoncus perpendicularis (Reich, 1797)			1	2.8	2	5.6	3
Rhinusa antirrhini (Paykull, 1800)					5	13.9	5
Rhinusa asella (Gravenhorst, 1807)	1	2.9					1
Rhinusa melas Boheman, 1838					1	2.8	1
Rhinusa neta (Germar, 1821)					4	11.1	4
Rhinusa tetra (Fabricius, 1792)			18	8.3	1	2.8	19
Rhyncolus punctatulus Boheman, 1838			1	2.8			1
Sciaphilus asperatus (Bonsdorff, 1785)	4	8.8	1	2.8	4	8.3	9
Sibinia pellucens (Scopoli, 1772)			2	5.6			2
Sibinia viscariae (Linné, 1761)			23	16.7			23
Sirocalodes depressicollis (Gyllenhal, 1813)			1	2.8			1
Sitona cambricus Stephens, 1831	3	5.9					3
Sitona hispidulus (Fabricius, 1777)	1	2.9	2	5.6	18	22.2	21
Sitona humeralis Stephens, 1831	10	5.9	1	2.8	2	2.8	13
Sitona lepidus Gyllenhal, 1834	*** 209**	**82.4**	16	22.2	**109**	**72.2**	334
Sitona lineatus (Linné, 1758)	1	2.9	1	2.8	17	27.8	19
Sitona sulcifrons argutulus Gyllenhal, 1834	**29**	26.5	*** 372**	**91.7**	54	19.4	455
Trachyphloeus angustisetulus Hansen, 1915			1	2.8			1
Trachyphloeus aristatus (Gyllenhal, 1827)			5	8.3			5
Trachyphloeus bifoveolatus (Beck, 1817)			4	8.3			4
Trichosirocalus rufulus (Dufour, 1851)					5	13.9	5
Trichosirocalus troglodytes (Fabricius, 1787)	11	8.8	1	2.8	18	25	30
Tychius breviusculus Desbrochers, 1873	3	2.9	1	2.8	8	16.7	12
Tychius meliloti Stephens, 1831	**28**	8.8	12	11.1	14	11.1	54
Tychius picirostris (Fabricius, 1787)	**64**	**73.5**	**54**	**55.6**	*** 235**	**88.9**	353
Tychius pusillus Germar, 1842	7	11.8	2	5.6	**62**	**72.2**	71
Tychius stephensi Schönherr, 1836			1	2.8	3	2.8	4
Xylosandrus germanus (Blandford, 1894)			1	2.8			1
Zacladus geranii (Paykull, 1800)					1	2.8	1
Dryophthoridae							
Sitophilus oryzae (Linné, 1763)					1	2.8	1
Sitophilus zeamais Motschulsky, 1855			1	2.8			1
Erirhinidae							
Tanysphyrus lemnae (Paykull, 1792)	1	2.9					1
Nanophyidae							
Hypophyes pallidulus (Gravenhorst, 1807)			3	8.3			3

Nanophyes brevis brevis Boheman, 1845	2	5.9			1	2.8	3
Nanophyes brevis fallax Rey, 1893			3	8.3			3
Nanophyes helveticus Tournier, 1867			9	22.2			9
Nanophyes marmoratus (Goeze, 1777)	3	5.9	1	2.8	2	5.6	6
Raymondionymidae							
Ferreria marqueti (Aubé, 1863)	2	2.9			1	2.8	3
Individuals/**total individuals**	841		840		1767		**3448**
Species/**total species**	64		68		82		**129**

7

Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland

Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland

Daouda Kouakou [1, 2], Thomas Sattler[1, 3], Martin K. Obrist[4], Peter Duelli[4], Marco Moretti[1]

[1] Swiss Federal Research Institute WSL, Ecosystem Boundaries, Via Belsoggiorno 22, CH-6500 Bellinzona, Switzerland

[2] Lamto Tropical Ecology Research Centre, Postal Box 28, Ndouci, Ivory Coast

[3] Zoological Institute, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[4] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

Published in *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 81: 191-198.

7.1 Abstract

We report the capture of two bee species new to Switzerland, *Anthidium florentinum* (Fabricius, 1775) and *Stelis simillima* (Morawitz, 1876), and of three rare species, *Coelioxys echinata* (Förster, 1853), *Lithurgus chrysurus* (Fonscolombe, 1834) *and Lasioglossum discum* (Smith, 185). All specimens were collected within the city limits of Lugano in the course of the project "BiodiverCity" of the Swiss NRP54. Identical collecting efforts in the cities of Zürich and Lucerne did not yield any new or very rare bee species. The known distribution and ecology of the reported five prevalently Mediterranean species are summarized.

Key words

Hymenoptera, Apidae, wild bees, distribution, urban environment.

7.2 Introduction

Thanks to the investigations of several apidologists in the last decades, the faunistic composition of wild bees (Hymenoptera, Apidae) in Switzerland is relatively well known (Amiet 1996, Schwarz et al. 1996, Müller et al. 1997, Amiet et al. 1999, 2001, 2004, 2007 & in press). The occurrence of 610 wild bee species (Hymenoptera, Apidae) from 41 genera and 7 subfamilies is documented for Switzerland. However, the knowledge on the bee fauna in urban areas in Switzerland is still limited (F. Amiet and A. Müller, personal communications) as this habitat type has rarely been included in faunistic surveys. This is even more true for the southern part of the Alps, where only a very limited number of bee studies have taken place (Amiet & Moretti, 2002, M. Abderhalden, personal communication). The present study was part of a larger National Research Program (NRP54). In the project BiodiverCity, which investigates biodiversity and its human perception in urban landscapes, we captured bee species in the three Swiss cities Zürich, Luzern and Lugano, which for Central European standards are of small to medium size. We present two new species to the Swiss bee fauna (Hymenoptera, Megachilidae), indicate new findings of three rare bee species (Hymenoptera, Megachilidae, Halictidae), and discuss the question whether they are recent immigrants or had been overlooked so far.

7.3 Materials and methods

This study was conducted on 106 sampling sites in the Swiss cities of Zürich (47°22 N, 8°31 E), Lucerne (47°05 N, 8°17 E), and Lugano (46°07 N, 8°56 E) from June 13th to August 3rd 2006. In Lucerne, 34 sampling locations were chosen, in Lugano and Zürich each 36. The locations were chosen to cover as widely as possible the total diversity along the three habitat quality gradients "age of green area", "sealed and built area" in a radius of 50 m, and "human management" (measured by the frequency of meadow mowing within 5 m around the trap).

Bees were sampled with one so-called combination trap (Duelli et al. 1999) and three pitfall-traps at each location. The combination trap combines a window interception trap with a yellow water pan and was placed at a height of 1.5 m above ground. The pitfall traps consisted of plastic cups recessed into the soil (opening diameter 75 mm), arranged in an isosceles triangle at a distance of one meter. Both, pitfall (for surface fauna) and combination traps (for flying insects) were filled with 0.2% Metatin (bactericide) solution. The combination trap and the pitfalls were installed exactly the same way at each of the 106 sites. The minimum distance between sites within a single town, and between the sites and the town margin, was 250 m. All traps were operated for seven weeks (from 24 June to 8 August 2006) according to the Rapid Biodiversity Assessment scheme (RBA; Duelli and Obrist 2005). In this period of the growing season the highest fraction of insect species present can be assessed with the least effort. Traps were emptied weekly and kept in 70% alcohol. In the lab, the insects were sorted to order or family level.

Bee species were identified according to the bee identification keys provided for Switzerland (Amiet 1996, Amiet et al. 1999, 2001, 2004, 2007, and in press.). Additionally, single specimens could be verified in the bee collection at the Department of Applied Entomology of the Swiss Federal Institue of Technology in Zürich and in the private collections of A. Müller and F. Amiet, and were confirmed by these specialists. The nomenclature is following the same literature as used for identification. Detailed information on synonymous species names is given in Table 1.

7.4 Results

The project BiodiverCity yielded a total of 142 species of Apoidea (104 in Lugano, 77 in Luzern, and 80 in Zürich) and a mean of 16.5 species per trap site. These data will be treated elsewhere. Here we focus on five very rare or new species for Switzerland. All these were found in the city of Lugano only (46°0 N 8°56 E), the most southern of the three investigated cities. Trap locations and collecting data are given in Fig. 1.

Two species new to the Swiss fauna were collected: Of *Anthidium florentinum* (Fabricus, 1775), belonging to the family Megachilidae, a single female was found in the western part of Lugano. Two females of *Stelis simillima* (Morawitz, 1876), also belonging to the megachilid family, were trapped in the Northwest and South of Lugano.

Three species are very rare in Switzerland: A single female of the extremely rare species *Coelioxys echinata* (Förster, 1853) was found in southern Lugano.

Overall, twelve individuals of *Lithurgus chrysurus* (Fonscolombe, 1834) were captured at eight locations. While three females were recorded at three different locations, eight males were sampled at seven locations spread all over Lugano.

One specimen of *Lasioglossum discum* (Smith, 1853) was found on a ruderal area in the center of Lugano.

7.5 Discussion

Had the two new species and the three very rare species been overlooked so far in Switzerland, or are they recent immigrants – maybe a testimony of global warming? Before giving a tentative answer to this question, we summarise what is known on the distribution and ecology of the five species.

Anthidium florentinum (Fabricius, 1775)

This bee species new to Switzerland is a predominantly Mediterranean species belonging to the family Megachilidae. In the North it reaches as far as Southern France (Rasmont et al. 1995; Banaszak & Romasenko, 1998), its southern limits are found in Morocco (Friese, 1898; Warncke, 1980; Wirtz et al. 1992). Thus the present record is the northern most observation of this species in its range. According to Müller (1996) and Banaszak & Romasenko (1998), *A. florentinum* is polylectic and forages pollen from Fabaceae and Lamiaceae as the preferred sources. However, the species preferred Rubus (Rosaceae) in Italy (Müller, 1996). Its presence in Switzerland had to be expected, given its occurrence in the neighboring countries Italy and France. Thanks to its proximity to the Mediterranean region, the city of Lugano experiences a warm and dry climate from June to August. Such climatic conditions favour the occurrence of this univoltine species flying from June to August (Amiet et al. 2004).

Stelis simillima (Morawitz, 1876)

According to detailed studies of Müller (1996) and Amiet et al. (2004) Stelis simillima is a well known Mediterranean bee species. There is still no published information on its occurrence in Germany and Austria. The discovery of *S. simillima* was expected for Switzerland for quite some time (F. Amiet, personal communication) and was therefore included in the Apidae handbook of Switzerland (Amiet et al. 2004). *S. simillima* is a cleptoparasite of the genus Lithurgus (Banaszak & Romasenko, 1998, Amiet et al. 2004). This species visits flowers for nectar only. It was reported to visit the Asteraceae *Centaurea solstitialis* (Rasmont et al. 1995). The two specimens were found more than two kilometer apart from each other, so they are likely to stem from different populations.They were found in the same locations where also their possible nest host *Lithurgus chrysurus* (Table 2 and Fig. 1) and several specimens of the genera Anthidium, Chelostoma and Osmia had been found (Kouakou et al., unpublished data). According to Amiet et al. (2004), this univoltine species flies in July and August. Detailed information on synonymous species names is given in Tables and figures.

Coelioxys echinata (Förster, 1853)

C. echinata has been found in Algeria, Morocco, Spain, Portugal, Caucasus, Russia, Sicily and Turkey (Ascher et al. 2007). The finding of a single female specimen of *C. echinata* in Lugano confirms its very rare presence in Switzerland, where it had been recorded only once since 1970, at Russin close to Geneva (Amiet et al. 2004). There are three old records from Ticino and Mesocco. The rediscovery of *Coelioxys echinata* in urban areas of southern Switzerland illustrates the capacity of urban habitats with their particular climate to sustain a variety of otherwise rare bee species. *C. echinata* parasitizes Megachilidae species, notably *Megachile apicalis* and *Megachile rotundata* (Amiet et al. 2004), as well as bees from the genera

Anthophora, Centris and Euglossa (Michener, 2000). This univoltine bee species is flying from July to August (Amiet et al. 2004).

Lithurgus chrysurus (Fonscolombe, 1834).

This species is widely distributed along the northern Mediterranean coast from Spain to Turkey and Israel, extending northwards to Germany, Slovakia and Austria, eastwards to the Caucasus and westwards to France (Ascher, 2005). Six specimens of this species have been recorded until 1969, and since 1970 it was rarely collected in southern Switzerland (Amiet et al. 2004). After that it has been classified as critically endangered (Amiet 1994). *L. chrysurus* is strictly oligolectic on Centaurea pollen (Rust et al. 2004) and flies from June to August. This new record of eleven specimens (3 females and 8 males) from eight locations in Lugano confirms its established occurrence in Switzerland and indicates that the species might have a wider distribution in Ticino than previously thought.

Lasioglossum discum (Smith, 1853)

This species, although very rare in Switzerland, has a wide distribution range including Morocco, Tunisia, Austria, Southern France, Israel, Italy, Spain, Kyrgyzstan, Romania, Slovenia, Turkey, and former Yugoslavia (Ascher et al. 2007). In these areas the species is rather abundant and widely distributed, whereas Switzerland is at the northern border of its geographical distribution. Accordingly, most of the Swiss specimens had been collected south of the Alps. *L. discum* is currently classified as an endangered species (Amiet et al. 2004).

7.6 Conclusions

We provide occurrence data on five bee species that are very rare or even new to Switzerland. The two new species augment the total number of Swiss bee species (Apidae) to 612. Despite the same capture effort in Zürich and Lucerne we found these five species only in the urban areas of Lugano. In the light of this result we may have to dismiss the hypothesis that these species were formerly overlooked urban inhabitants. More likely, Lugano is a first Swiss stepping stone for a Mediterranean insect fauna adapted to hot and dry summers and mild winters. So far the insubric climate of Ticino had been too wet for many potential immigrants among the Mediterranean insects. Since the climate in cities is generally warmer and drier than that in the surroundings, the cities tend to be the first habitats to harbour immigrant thermophilous species. These species may eventually spread to areas outside of cities when climate warming provides suitable temperature regime. We consider wild bees in cities as an enrichment for urban biodiversity as well as for the surrounding region. We suggest that urban areas be managed in ways that maintain meadows which provide nectar and pollen, as well as microhabitats which offer nesting opportunities for wild bees.

Acknowledgements

We thank Felix Amiet (Solothurn) and Dr. Andreas Müller (ETH, Zurich) for their continuous support and hospitality, and for confirming the identifications. Thanks are due also to Mike Herrmann for identification work, Christophe Praz and Sebastien Patiny for providing literature, and to Barbara Krummenacher for feeding the database. This research was supported by a grant from the Swiss Federal Commission Scholarship for Foreign Student and Swiss embassy in Côte Ivoire. The overall project “BiodiverCity” was funded by the Swiss National Science Foundation in the framework of the National Research Program NRP54 "Sustainable development of the built environment" (www.nfp54.ch).

7.7 References

Amiet, F. 1994. Liste rouge des abeilles menacées de Suisse. In: P. Duelli (Ed.), Rote Liste der gefährdeten Tierarten der Schweiz, pp. 38-44. – Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern.

Amiet, F. 1996. Hymenoptera, Apidae, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, die Gattungen Apis, Bombus und Psithyrus. – Schweizerische Entomologische Gesellschaft, Neuchâtel, 98 pp.

Amiet, F., Müller, A. & Neumeyer, R. 1999. Apidae 2. Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha. – Schweizerische Entomologische Gesellschaft, Neuchâtel, 219 pp.

Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2001. Apidae 3. Halictus, Lasioglossum. – Fauna Helvetica, CSCF, SEG, Neuchâtel, 208 pp.

Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2004. Apidae 4. Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis. – Fauna Helvetica, CSCF, SEG, 273 pp.

Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2007. Apidae 5. Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa. – Fauna Helvetica, CSCF, SEG, 356 pp.

Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. In press. Apidae 6. Andrena, Melitturga, Panurginus und Panurgus. Fauna Helvetica, CSCF, SEG.

Amiet, F. & Moretti, M. 2002. Neue und interessante Bienen- und Wespenarten für das Tessin und die Schweiz von Waldrandgebieten (Hymenoptera: Aculeata: Apidae, Pompilidae, Sphecidae). – Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 75: 183-189.

Ascher, J. 2005. – linked at: http://www.discoverlife.org/mp/20m?kind=Lithurgus+chrysurus

Ascher, J., Connal, E., Griswold, T., Melo, G., Polaszek, A., Ruggiero, M., Williams, P., Walker, K., & Warrit, N., 2007. – linked at: http://www.discoverlife.org/mp/20q?act=x_guide_credit&guide=Apoidea_species

Banaszak, J., & Romasenko L. 1998. Megachilid bees of Europe (Hymenoptera, Apoidea, Megachilidae). – Pedagogical University, Bydgoszcz (Poland), 239 pp.

Duelli, P., Obrist, M.K. & Schmatz, D.R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. – Agriculture, Ecosystems and Environment, 74: 33-64.

Duelli, P. & Obrist, M.K. 2005. Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). – Schriftenreihe der Forschungsanstalt Reckenholz, 56: 132–38.

Friese H., 1898. Die Bienen Europa's (Apidae europaeae). Theil V. Solitäre Apiden: Genus Lithurgus, Genus Megachile (Chalicodoma). In: Rasmont P., Ebmer P.A., Banaszak J., & Zaden G. 1995. Hymenoptera Apoidea Gallica. Liste taxonomique des abeilles de France, de Belgique, de Suisse et du Grand-Duché de Luxemburg. – Bulletin de la Société entomologique de France, 100: 1-98.

Michener C.D. 2000. The Bees of the World. – The John Hopkins University Press, Baltimore and London, 913 p.

Müller, A., 1996. Host-plant specialization in western Palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae). – Ecological Monographs, 66: 235–257.

Müller, A., Krebs, A. & Amiet, F. 1997. Bienen • Mitteleuropäische Gattungen, Lebensweise, Beobachtung. – Naturbuch Verlag, Augsburg.

Müller, A., 2002. *Osmia (Melanosmia) steinmanni sp.n.*, a new bee species from the Swiss Alps (Hymenoptera, Apoïdea, Megachilidae). – Revue Suisse de Zoologie, 109(4): 803-812

Rasmont P., Ebmer P.A., Banaszak J., & Zaden G. 1995. Hymenoptera Apoidea Gallica. Liste taxonomique des abeilles de France, de Belgique, de Suisse et du Grand-Duché de Luxemburg. – Bulletin de la Société entomologique de France, 100: 1-98.

Rust, R.W., Cambon, G., Grossa, T., & Vaissière, B.E. 2004. Nesting biology and foraging ecology of the wood-boring bee *Lithurgus chrysurus* (Hymenoptera: Megachilidae). – Journal of the Kansas Entomological Society, 77(3): 269–279.

Schwarz, M., Gusenleitner, F., Westrich, P. & Dathe, H. 1996. Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae). – In: Entomofauna (Linz), Supplement 8: 398 pp.

Warncke, K. 1980. Die Bienengattung Anthidium Fabricius, 1804, in der Westpaläarktis und im turkestanischen Becken. –Entomofauna 1: 119-209.

Wirtz, P., Kopka, S., & Schmoll, G. 1992. Phenology of two territorial solitary bees, *Anthidium manicatum* and *A. florentinum* (Hymenoptera: Megachilidae). – Journal of Zoology (United Kingdom) 228(4): 641-651.

7.8 Tables and figures

Table 1: Species names and their synonyms.

Species	**Synonyms**
Anthidium florentinum (Fabricius, 1775)	*Anthidium florentinum* var. *hispanicum* Mocsary, 1884 *Anthidium florentinum* var.*rufescente* Dusmet, 1908 *Anthidium florentinum* var. *kissi* Alfken, 1935 *Anthidium subspinosum* Klug, 1832
Stelis simillima (Morawitz, 1876)	*Stelis cognata* Kohl, 1892 *Stelis genalis* Pasteels, 1969
Coelioxys echinata (Förster, 1853)	*Coelioxys rufocaudata* (Smith, 1854) *Coelioxys octodentata* (Lepeletier, 1841)
Lithurgus chrysurus (Fonscolombe, 1834)	*Chrysurus* var. *siculus* (Pérez, 1897) *Lithurgus haemorrhoidalis* Lepeletier, 1841
Lasioglossum discum (Smith, 1853)	ssp. *discum* (Smith 1853) *Halictus discus* Smith, 1853 *Halictus morbillosus* Kriechbaumer, 1873 *Halictus morbillosus glasunovi* Cockerell, 1924 *Halictus fertoni* Vachal, 1895 *Lasioglossum pseudomorbillosum* Ebmer 1970 ssp. *fertoni* (Vachal,1895)

Table 2: Bee species that are very rare or new to Switzerland and the coordinates of their respective locations in Lugano. * = new to Switzerland, ** = rare species

Species	**Coordinates (Swiss grid system)**
* *Anthidium florentinum* Fab. 1 ♀	716502/97079
* *Stelis simillima* Mor. 2 ♀♀	718269/98081
	716294/96132
***Coelioxys echinata* För. 1 ♀	718608/96306
***Lithurgus chrysurus* Fon. 3 ♀♀, 8 ♂♂	718269/98081
	717201/97164
	716196/95873
	716502/97079
	717097/97295
	717255/96948
	718608/96306
	718470/97494
***Lasioglossum discum* Smit. 1 ♀	717980/96810

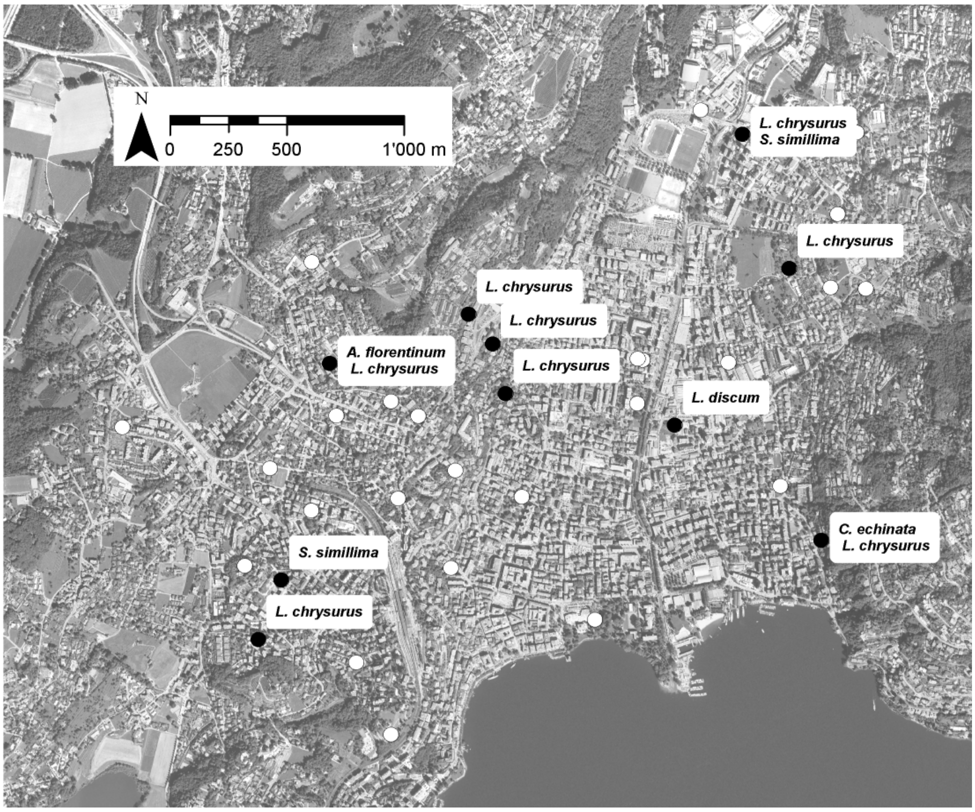

Fig. 1: Distribution of rare species and species new to Switzerland in Lugano. Black dots: locations with new or rare species; white dots: locations with no new or rare species.

8

General Conclusions

I summarise the conclusions of my PhD on urban biodiversity regarding ‘total species richness’ (chapters 2 & 3), species composition (chapter 4), and single species (chapters 5-7).

8.1 Species richness

In all taxonomical groups studied in greater detail (Apidae, Araneae, Aves, Chiroptera, Curculionidae), we found substantial fractions (12-50%) of the total known species numbers in Switzerland (Gamma diversity; Table 1). Additionally, we can compare – with some caution – the local species richness (Alpha diversity) of arthropods analysed with Rapid Biodiversity Assessment of our urban sampling locations with those of other environments outside cities, where the same method was applied (Duelli and Obrist 2005, Obrist and Duelli submitted): The arthropod numbers obtained in cities (mean 284 species; range 169-361) are in between the ones from forests (mean 232 species; range 69-473) and agricultural areas (mean 317 species; range 161-470). Local species richness for birds averaged at 15.2 species per sampling location (SD = 3.9; range = 7 – 25) with only small variation between the three cities. These results confirm the numerous studies which showed high species richness in urban areas for most taxonomic groups (e.g. plants (Sukopp et al. 1979, Landolt and Hirzel 2001, Thompson et al. 2004); arthropods (Klausnitzer 1988, Bolger et al. 2000, McIntyre et al. 2001, Niemela et al. 2002, Smith et al. 2006); birds (Blair 1999, Marzluff 2001, Evans et al. 2009); bats (Gaisler et al. 1998, Gehrt and Chelsvig 2004, Scanlon and Petit 2008). Even though studies on a rural – urban gradient show that species numbers of most taxonomic groups decrease heavily towards the densely built city centres (see McDonnell and Hahs 2008) for a review), quite a number of urban habitats seem to support many species.

However, in the arthropod study (chapter 1) we found the striking result that total species numbers as well as species richness of the functional groups (trophic, pollinator and mobility guilds) are surprisingly robust to changes from supposed good (e.g. meadows cut only 2-3 times/year) or bad (e.g. highly sealed) habitats. We found that heterogeneous habitats, meaning many different (vegetation) structures at close distance, host the highest species numbers of arthropods, probably due to the underlying structural and floral diversity. The fine-grained spatial inter-linkage of bad (sealed) with good (heterogeneous) habitats in urban areas, generally referred to as the urban mosaic (Rebele 1994), is probably the key feature responsible for the observed robustness of arthropods to changes in habitat quality (along the gradients age, management, sealed area). I conclude from these results that the highly fragmented nature of urban areas may not represent a major obstacle for the arthropods currently existing in cities, because they have probably been selected for tolerance to fragmentation and for high colonisation potential. We used passive sampling of mostly flying insects. An active sampling method in comparatively short time spans might have resulted in a measurement of closer species-habitat associations.

For bird species richness, the main structures responsible for a high diversity are trees, preferably in a good mix of broadleaved and coniferous plants (chapter 2). Our models predict an increase from 13 bird species in the absence of trees to 20 species with 46% tree cover. They also predict an increase from 14 bird species in places with deciduous woody plants only, to 20 species in places where coniferous and deciduous plants occur in equal abundances. In Central European nature conservation, coniferous trees are often regarded as bad for biodiversity, as most species are non-native (either from the Alps or from exotic countries). Our results might offer the possibility to rethink this dogma and decide upon the use of coniferous trees depending on ecosystems, i.e. the use could be different in forests and urban areas.

8.2 Community Composition

Based on the results of chapters 2 and 3, I expected to obtain a more comprehensive appraisal of the environmental variables structuring urban biodiversity when analysing community composition of ecologically different groups such as spiders, bees and birds (chapter 4). In addition to community – habitat associations, we wanted to identify the relative importance of environmental and biotic processes in urban habitats, which has not yet been investigated in this environment. Biotic processes such as dispersal and interspecific competition lead to spatially autocorrelated species distributions. This phenomenon is named 'neutral theory of biodiversity' (Bell 2000, Hubbell 2001) and is somewhat opposed to the classical 'environmental control theory' (Hutchinson 1957). Recent studies, however, have shown that both processes work synergistically to shape community compositions in ecosystems (Legendre et al. 2009). Our results in urban ecosystems demonstrate the near absence of any spatial organisation (which could be due to both biotic processes and environmental variables, which themselves are spatially organised) in species communities of all three taxonomical groups. This finding suggests that biotic processes play a subordinate to negligible role in structuring spider, bee and bird communities in urban areas, leading to the conclusion that the neutral theory might not be important in urban areas. We suggest that the manifold human activities in urban areas inhibit both the development and installation of spatially organized environmental variables and of biotic processes.

Overall, the results of this chapter confirm the results of chapters 2 and 3 in that most species occurring in urban areas are not constantly struggling to survive in this habitat type, but probably have undergone selection to cope with the heavy human influences such as high fragmentation and regular habitat disturbances. Stochasticity plays an important role in 'controlling' urban species communities. Community composition in urban areas must be considered as far from equilibrium and in constant change to adapt to the turbulences that characterize this environmental type.

Based on these results I expect a typical urban species to be a 'flexible' species, possibly living in several habitat types and/or having the means to reproduce quickly (r-strategy). Therefore, communities should be dominated by generalist species that are not limited to a great extent by the fragmented nature of urban habitats. The thriving of generalist species in urban areas has actually been described for several taxonomic groups (Jonsen and Fahrig 1997, Gibb and Hochuli 2002, Niemela et al. 2002, Ishitani et al. 2003, Devictor et al. 2007). The increase of the same generalist species in cities all over the world has been termed as 'biotic homogenisation' and has received great attention in the past few years (Blair 2001, Jokimaki and Kaisanlahti-Jokimaki 2003, La Sorte and McKinney 2007, McKinney 2008, Sorace and Gustin 2008); in 2006, the journal 'Biological Conservation' even published a special issue on this topic (e.g. Kuhn and Klotz 2006, McKinney 2006, Olden et al. 2006, Pauchard et al. 2006).

8.3 Species

Studies on the species level enable us to gain more detailed information on the interplay between species and their urban environment. Chapters 5-7 each treat a single species from a different taxonomical group (bats, weevils, rare bees).

The study on bats (chapter 5) again includes an analysis of the relative contribution of environmental and spatial variables. In strong contrast to the previous study on the community level of spiders, bees and birds, the results on bats highlight the fact that spatial information explains significant portions of total variation in bat occurrence and activity. The spatial distribution of roosts critically determines the bats' occurrences when hunting in urban areas. All six species regularly found in cities are aerial hawkers that search patches of high prey abundance and prey there opportunistically on the most abundant flying insects; thus, with regard to their foraging behaviour, these species are mainly generalists. This characteristic makes them typical urban species.

The generally warmer temperature in cities has been described as the Urban Heat Island effect (Pickett et al. 2001), which creates special habitat conditions in urban areas. This climatic quality resembles living conditions outside cities (e.g. xerothermic or Mediterranean conditions) but in combination with urban habitat types such as fertile lawns or buildings, the higher temperatures creating a unique and new environment.

These typical urban conditions favour both the autonomous invasion of termophilous species and the enhanced survival of species introduced by man. An example for the latter is found in the weevil study (chapter 6). It is strongly suspected that the blind and edaphic weevil *F. marqueti*, which has been found in Zurich and Lucerne, was transported in soil or among roots of garden shrubs to city gardens. In our study, we also found several insect species that stem from outside of Europe and represent exotic and sometimes even invasive species. In the weevil study we found *Sitophilus zeamais*, which is a synanthropic, worldwide crop pest. In Zurich we found the true bug *Halyomorpha halys* (Heteroptera), which originally comes from South-east Asia. Its findings are among the first in Europe and the species seems to have detrimental effect on ornamental shrub species (Wermelinger et al. 2008). The invasive potential of the introduced Asian ladybird *Harmonia axyridis* (Coccinellidae) with negative effect on native ladybird species is already well known (Brown et al. 2008). We found the species regularly in all three study cities.

Species invasions facilitated by urban areas are not a novel phenomenon but have probably existed since the early days of urban settlements (Ineichen 1997). The BiodiverCity project unravelled some new or at least previously unknown developments. Again, in the study on weevils, we found that this community is dominated by the xero-thermophilous species *Protapion trifolii*, which previously was considered to be restricted to natural habitats such as warm, calcareous grasslands in Switzerland. This species either survived in remnants of semi-natural grasslands within the city fringe and consequently spread to urban lawns and meadows, or immigrated into the cities from surrounding grasslands.

Other species have invaded cities from more distant areas such as the Alpine arch or the Mediterranean area. Despite the fact that it is often difficult or impossible to disentangle the effects of a ‘natural’ range expansion and the effects of a higher temperature, we can note that cities have at least a supportive function in the settlement process of immigrant species into temperate latitudes; for quite a few of them, urban areas represent a 'point of origin' for further spreading and settlement. This is the case in the two bat species *Pipistrellus kuhlii* and *Hypsugo savii*. Since approximately twenty years ago, *P. kuhlii* has invaded cities north of the Alps from the Mediterranean. Over this time period, *P. kuhlii* populations grew fast, often surpassing the populations of the previously most common urban species, *P. pipistrellus*. Thanks to the good urban populations, this species has started to populate even villages in recent years. That *H. savii* regularly inhabits Swiss cities was found for the first time by the BiodiverCity project, reflecting a recent establishment in the study cities north of the Alps. *H. savii* originally roosted in rocks and cliffs in the Southern Alps and the Mediterranean. Densely built areas and warm temperatures reflect an artificial but suitable environment for this bat species. It started to use an ecological niche that is occupied by the bird *Apus melba* during day time, also a species with an originally Southern distribution.

In chapter 7, we describe the occurrence of five rare and prevalently Mediterranean bee species (*Anthidium florentinum* and *Stelis simillima* are new to Switzerland). Despite the same capture effort, we found these species only in the southernmost study city of Lugano, but not in Zurich or Lucerne. We suggest that Lugano is a first Swiss stepping stone for a Mediterranean insect fauna adapted to hot and dry summers and mild winters.

These examples illustrate that cities, thanks to their warmer climate, offer special and new habitat conditions that are continuously explored by species. When found suitable, the colonisers will exploit the newly found niches. In this way, cities potentially anticipate changes in fauna that will eventually happen in other environments with ongoing global warming.

In conclusion, I emphasise that cities should not be regarded as environments more hostile for biodiversity than other environments; they should not be underestimated in the quality they may host. Depending on the species' ecology, they offer favourable and less favourable environmental conditions, similar to any other ecosystem. Some species even thrive in cities, as the dense mosaic of different habitats and warm-dry climatic conditions provides optimal biotopes. They may also benefit from new opportunities arising in the urban environment (e.g. abundant food, predator release). Urban fox populations in Swiss cities reach densities that are up to ten times higher than in the alpine habitat (Gloor et al. 2001). In the United Kingdom it has been found that birds reach densities in urban areas that are six times as high as in the countryside (Fuller et al. 2009).

However, I point to the fact that species occurring in urban areas are rarely species of conservation concern. Thus, offering habitats in cities cannot replace biodiversity protection outside the city fringe. In this context, I would also like to remind the reader that the decision to save an individual species with special conservation efforts is mainly a question of values (see introduction) and usually not an ecological necessity per se. Nevertheless, it is of the highest importance that biodiversity in urban areas is maintained or even enhanced. After having worked on this topic for several years, I am now convinced that by far the **most important reason to protect urban biodiversity is to provide opportunities for urban residents to experience nature.** Such experiences are essential for a) the individual well-being of city inhabitants (Fuller et al. 2007), and – since personal experiences influence people’s values and opinions – for b) political decisions regarding environmental conservation in general (Turner et al. 2004).

8.4 Practical implications

Based on the results of my PhD, I can derive a) several practical measures and b) additional issues that need to be considered when enhancing urban biodiversity. I would like to start with the latter:

- The most important thing to keep in mind when preparing to take measures to enhance urban biodiversity: Cities are habitats built by and for humans. No living organism accepts deterioration of its habitat. Thus, actions in favour of biodiversity will only persist if from the outset, they take into account the use and perceptions of their human inhabitants.

- This fundamental understanding may be seen as a limitation on what actually can be done to improve biodiversity in cities. But at the same time it gives us a very strong argument. The parallel PhD in Social Science within the BiodiverCity project showed that city residents like a diverse physical environment consisting of different elements such as trees, shrubs, meadows, lawns, flowers etc. (Fig. 1; Home et al. in Press). This result indicates that urban biodiversity and human requirements for good urban habitats are aligned. These are important messages for city planners and managers willing to positively influence urban biodiversity.
- If the urban green is built according to these human needs, the resulting urban landscapes will offer the heterogeneous habitats that are needed for a rich urban biodiversity.
- There is some evidence that the highly fragmented nature of urban areas may not represent a major obstacle for many urban species, because they have probably been selected for tolerance to fragmentation and for high colonisation potential. This implies that urban habitats – allowed a minimum time – will be rather rapidly populated by them (including possible invasive species). Additionally, this means an evaluation of the effects of conservation measures with simple indicators such as species richness might be difficult due to the robustness of urban biodiversity. Such a monitoring would need to aim at selected focal species
- There is – not surprisingly, but to the disappointment of politicians – no unique management option that will improve all aspects of urban biodiversity. Decisions according to values (see introduction) must be taken.
- Given the increasing densification of urban areas, the already high human pressure on the remaining natural spaces will become even greater. Nevertheless, our results have shown that there is still quite a

high potential for measures – a surprisingly high number of, often small, areas are not directly used by humans and lend themselves to improvements. Our suggestions may provide some guidance for that endeavour. As a political driver there is the promise to achieve not only an improvement of habitats and of the diversity of flora and fauna, but also of the life quality of the residents.

8.5 Practical measures

- Planning the remaining urban green as heterogeneous habitats, and managing it as extensively as the local human exigencies allow it, will benefit virtually all arthropod groups.
- Increasing the diversity of insects and spiders can be done on fine scales and thus by individual households. Improving the heterogeneity in small areas is a promising measure even at comparatively high densities of buildings and roads.
- Planting trees and bushes is the best measure to enhance bird species diversity. A good mix of coniferous and deciduous woody plants maximises bird species richness but may lower habitat quality for specialists of deciduous parklands.
- Bat results highlight the importance of the spatial component and the large scale habitat composition for this species group. The planning and creation of balanced urban areas with highly overbuilt areas interspersed with urban green and water promotes the presence of these insectivore predators.
- With the expected increasing urban densification, novel options should also be evaluated to conserve and improve biodiversity in the urban context under more restricted conditions. One of the options is the ‘vertical green’, i.e. planned green structures on possibly several physical levels (several green roofs on top of each other) or as specific green floors in multi-storey buildings.

8.6 References

Bell, G. 2000. The distribution of abundance in neutral communities. American Naturalist 155:606-617.

Blair, R. B. 1999. Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? Ecological Applications 9:164-170.

Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the U.S. Pages 33-56 in J. L. Lockwood and M. L. McKinney, editors. Biotic Homogenization. Kluwer, Norwell (MA).

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban habitat fragments in southern California: Area, age, and edge effects. Ecological Applications 10:1230-1248.

Brown, P. M. J., T. Adriaens, H. Bathon, J. Cuppen, A. Goldarazena, T. Hägg, M. Kenis, B. E. M. Klausnitzer, I. Kovář, A. J. M. Loomans, M. E. N. Majerus, O. Nedved, J. Pedersen, W. Rabitsch, H. E. Roy, V. Ternois, I. A. Zakharov, and D. B. Roy. 2008. *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. BioControl 53:5-21.

Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21:741-751.

Duelli, P. and M. K. Obrist. 2005. Eine preiswerte Methode zur Abschätzung der lokalen Arthropodenfauna: "Rapid biodiversity assessment" (RBA). Schriftenreihe der Forschungsanstalt Reckenholz 56:132-138.

Evans, K. L., S. E. Newson, and K. J. Gaston. 2009. Habitat influences on urban avian assemblages. Ibis 151:19-39.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3:390-394.

Fuller, R. A., J. Tratalos, and K. J. Gaston. 2009. How many birds are there in a city of half a million people? Diversity and Distributions 15:328-337.

Gaisler, J., J. Zukal, Z. Rehak, and M. Homolka. 1998. Habitat preference and flight activity of bats in a city. Journal of Zoology 244:439-445.

Gehrt, S. D. and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. Ecological Applications 14:625-635.

Gibb, H. and D. F. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106:91-100.

Gloor, S., F. Bontadina, D. Hegglin, P. Deplazes, and U. Breitenmoser. 2001. The rise of urban fox populations in Switzerland. Zeitschrift Fur Saugetierkunde-International Journal of Mammalian Biology 66:155-164.

Home, R., N. Bauer, and M. Hunziker. in Press. Cultural and Biological Determinants in the Evaluation of Urban Green Spaces. Environment and Behavior.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson, G. E. 1957. Concluding remarks. Pages 415–427 in Harbor Symposium on Quantitative Biology, Population Studies: Animal Ecology and Demography, Cold Spring Harbour.

Ineichen, S. 1997. Die wilden Tiere in der Stadt. Waldgut Verlag, Frauenfeld.

Ishitani, M., D. J. Kotze, and J. Niemela. 2003. Changes in carabid beetle assemblages across an urban-rural gradient in Japan. Ecography 26:481-489.

Jokimaki, J. and M. L. Kaisanlahti-Jokimaki. 2003. Spatial similarity of urban bird communities: a multiscale approach. Journal of Biogeography 30:1183-1193.

Jonsen, I. D., and L. Fahrig. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12:185-197.

Klausnitzer, B. 1988. Verstädterung von Tieren. A.Ziemsen Verlag, Wittenberg Lutherstadt.

Kuhn, I., and S. Klotz. 2006. Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. Biological Conservation 127:292-300.

La Sorte, F. A. and M. L. McKinney. 2007. Compositional changes over space and time along an occurrence-abundance continuum: anthropogenic homogenization of the North American avifauna. Journal of Biogeography 34:2159-2167.

Landolt, E., and R. Hirzel. 2001. Flora der Stadt Zürich: 1984-1998. Birkhäuser.

Legendre, P., X. C. Mi, H. B. Ren, K. P. Ma, M. J. Yu, I. F. Sun, and F. L. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Marzluff, J. M. 2001. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston.

McDonnell, M. J., and A. K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23:1143-1155.

McIntyre, N. E., J. Rango, W. F. Fagan, and S. H. Faeth. 2001. Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52:257-274.

McKinney, M. L. 2008. Do humans homogenize or differentiate biotas? It depends. Journal of Biogeography 35:1960-1961.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247-260.

Niemela, J., D. J. Kotze, S. Venn, L. Penev, I. Stoyanov, J. Spence, D. Hartley, and E. M. de Oca. 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology 17:387-401.

Obrist, M. K. and P. Duelli. submitted. Rapid Biodiversity Assessment (RBA) of arthropods for monitoring average local species richness and related ecosystem services. Biodiversity and Conservation.

Olden, J. D., N. L. Poff and M. L. McKinney. 2006. Forecasting faunal and floral homogenization associated with human population geography in North America. Biological Conservation 127:261-271.

Pauchard, A., M. Aguayo, E. Pena, and R. Urrutia. 2006. Multiple effects of urbanization on the biodiversity of developing countries: The case of a fast-growing metropolitan area (Concepcion, Chile). Biological Conservation 127:272-281.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.

Rebele, F. 1994. Urban Ecology and Special Features of Urban Ecosystems. Global Ecology and Biogeography Letters 4:173-187.

Scanlon, A. T., and S. Petit. 2008. Effects of site, time, weather and light on urban bat activity and richness: considerations for survey effort. Wildlife Research 35:821-834.

Smith, R. M., P. H. Warren, K. Thompson, and K. J. Gaston. 2006. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15:2415-2438.

Sorace, A., and M. Gustin. 2008. Homogenisation processes and local effects on avifaunal composition in Italian towns. Acta Oecologica-International Journal of Ecology 33:15-26.

Sukopp, H., H.-P. Blume, and W. Kunick. 1979. The soil, flora and vegetation of Berlin’s wastelands. Pages 115-132 in I. C. Laurie, editor. Nature in Cities. John Wiley, Chichester.

Thompson, K., J. G. Hodgson, R. M. Smith, P. H. Warren, and K. J. Gaston. 2004. Urban domestic gardens (III): Composition and diversity of lawn floras. Journal of Vegetation Science 15:373-378.

Turner, W. R., T. Nakamura, and M. Dinetti. 2004. Global urbanization and the separation of humans from nature. Bioscience 54:585-590.

Wermelinger, B., D. Wyniger, and B. Forster. 2008. First records of an invasive bug in Europe: *Halyomorpha halys* Stål (Heteroptera: Pentatomidae), a new pest on woody ornamentals and fruit trees? Mitteilungen der Schweizerischen Entomologischen Gesellschaft 81:1-8.

8.7 Tables and figures

Table 1: Number of species found in the studies of BiodiverCity and total number of species known to currently live in Switzerland. For methodological reasons, the obtained fraction of the urban numbers on total species numbers in Switzerland represents the absolute minimum figures, especially for Apidae, Araneae and Curculionidae (only seven weeks sampled).

Scientific name	Common name	Number of species found in BiodiverCity	Total number of species known to be currently living in Switzerland	Fraction of BiodiverCity on total species numbers
Apidae	Bees	139	612	~23%
Araneae	Spiders	163	~945	~17%
Aves	Birds	63	~185 (breeding birds)	~34%
Chiroptera	Bats	14	28	50%
Curculionidae	Weevils	129	> 1050	~12%

A)

B)

C)

Fig. 1: The preferences of urban landscapes by the general Swiss public (taken from Home et al. in Press). Landscape A is the most preferred landscape of 21.5%, B of 20.2%, C of 19.8% of the population. People could chose from 12 different manipulated landscapes.

Acknowledgments

Congratulations, you either had great stamina and read through the thesis to reach this part of my PhD or you figured out which part is the most important one and more or less directly came here (I would have done it that way…). The acknowledgements, indeed, are the most important part of this document, because, all the results, the gained scientific knowledge, the detection of new species for Switzerland or other rare or common species, the basic or sophisticated analyses, the development of storylines for the individual chapters and then the writing could not have taken place without the help of numerous people. Throughout this large and complex project, I came in contact with many people who accompanied me in all possible ways in the last years. We discussed scientific and personal topics, exchanged ideas and ways of thinking, argued, worked together in the field, sorted insects and spiders, solved smaller or larger technical or statistical problems, prepared presentations, questionnaires, documents for the broad public, read and improved earlier versions of the chapters, exchanged emails. You supported me with logistics, food, mental encouragement or assisted me in any other possible way. Some of you, I met only on a 'virtual' basis, via email. To all of you:

Thank you, you made this thesis possible.

For a longer or shorter period you all have been BiodiverCitizens. I might have been able to convince you – either in our discussions or through this thesis –that maintaining or enhancing urban biodiversity is important – for our own sake.

I would like to thank the following people personally.

My supervisors

Marco Moretti, together with Fabio Bontadina and Marcel Hunziker you have initiated BiodiverCity and have given me the possibility to immerse into urban ecology. You gave tremendous efforts along this project and have not stopped thinking how things could be improved.

Martin Obrist, for being closest to this PhD, not only but also physically; you have been heavily involved in most aspects of it – planning, field work, lab work, analysis, writing. Your door has always been open for me.

Fabio Bontadina, long lasting companion in scientific and conservation matters and believing in me in the most critical period of this project; for your calm way of looking at the essential; I continue to learn from your expertise in communication to different target groups.

Peter Duelli, for being the 'grand, old patron' in this project; you combine serenity, knowledge and distance with regard to both, biodiversity and the business of science.

Raphaël Arlettaz, for decisive analytical input at critical milestones in this project; for having taken me on board of the 'CB' for my Master thesis and keeping me on the vessel for the PhD thesis.

Kevin Gaston, for having agreed on becoming the external supervisor and for having influenced my thinking through your numerous publications. I am looking forward to meeting you personally.

Laurent Excoffier, for the spontaneous agreement to chair the PhD defense.

Additional authors in specific chapters

You greatly added to my PhD in various aspects – I thank you very much: Simone Fontana for being 'my' Master student (University of Basel), eagerly learning about both, bird calls and R-scripts; Daouda 'the pinner' Kouakou, you came as an exotic stranger to the project and you left as a special friend; Christoph Germann, you were not only fast in determining 'your' weevils but also popped up with a first version of a manuscript 'out of the blue'.

Pierre Legendre and Daniel Borcard, you opened the door to your Numerical Ecology group in Montréal. You not only introduced me to the fascinating and challenging world of spatial statistics but continued supporting me back in Switzerland.

BiodiverCity Team

Robert Home, how much exchange did we have during these years learning about the fields of the other! Thank you for all the discussions, for coming along to the field and for improving the English of the manuscripts. Marcel Hunziker, Nicole Bauer, Paolo Della Bruna, Sandra Gloor and Stefano Wagner, you filled BiodiverCity with your expertise and lively presence.

Field work

While Alexandra Schulz, Vanessa Albin (both for their diploma thesis at Zurich University of Applied Sciences) and Franco Fibbioli collected the arthropods in Lugano, Peter Wirz and Beat Fecker helped me in Zurich and Lucerne. Barbara Krummenacher (diploma thesis Zurich University of Applied Sciences) and Felix Maurer helped in bat call recordings, Jordi 'the finger' Ambrosini took up environmental variables in the field and continously digitised them in GIS.

Charlotte Sattler, Martin Grüebler, David Koller and the Ehrler family offered any kind of logistical support in Lucerne.

Lab work

A whole army (of mainly women) supported me greatly in sorting the approximate number of 643’000 arthropods (equalling to 12.8 liters) to family and order level. Many thanks to Vanessa Albin, Vasyl Chumak, Wolfgang Kastenholz, Maria Kindermann, Laura Milani, Arlette Niederer, Michael Ryf, Alexandra Schulz, Regula Siegwart, Regula Tester.

This effort formed the basis for the identification work of the taxonomic specialists: Christian Bernasconi, Anya Rossi (both Formicidae), Claudio Canepari (Coccinelidae), Yannick Chittaro (Carabidae), Peter Duelli (Neuroptera), Christoph Germann (Curculionidae), Xaver Heer (Araneae), Daouda Kouakou, Felix Amiet, Andreas Müller, Mike Hermann (all Apoidea), Cinzia Pradella (Lucanidae, Buprestidae, Cerambycidae), Ferenc Vilisics

(Isopoda), Denise Wyniger (Heteroptera). Your skills and knowledge are greatly appreciated.

I am indebted to the following people for fruitful conceptual discussions and/or statistical advice: Thomas Fabbro, Fitsum Gebreselassie, Michael Schaub, Jerôme Pellet, Dieter Häring, Stefanie von Felten, Felix Kienast, Janine Bolliger, Miquel De Caceres Ainsa, Sapna Sharma, Tobias Roth, Martin Weggler and Felix Maurer.

In the final phase Robert Home, Niklaus Zbinden, Urs Kormann, Matthew Cartner, Stephanie Morris and Meta Lehmann supported me greatly in improving (the English in) the manuscripts or doing the layout.

I am thankful to Marco Conedera and Daniela Furrer from the WSL Research Unit 'Ecosystem boundaries' in Bellinzona for their continuous support. I am grateful to Christoph Scheidegger from RU 'Biodiversity and Conservation Biology' in Birmensdorf for the open doors and the generous hospitality. I thank the people from these RUs and the RU 'Ecological Genetics and Evolution' for their company, fruitful contacts, discussions and laughters. A special thank goes to Urs Kormann, Barbara Schlup, Kurt Bollmann, Thibault Lachat and my former and present office mates Matthias Albrecht, Sonja Braaker, Annie Ehrenbold and Saran Cheenacharoen.

I had enriching discussions inside and outside seminars with many people from the division of Conservation Biology, University of Bern. Thank you!

The authorities of Lugano, Zurich and Lucerne with their corresponding contact institutions Dicastero del territorio and Dicastero servizi urbani Lugano, Grün Stadt Zürich, Umweltschutzamt Luzern supported BiodiverCity from the start.

I would like to mention the Swiss railways SBB for the generally very smooth transportation and the comfort in their wagons when constantly moving between Zurich-Bellinzona-Lugano-Bern-Lucerne.

I am indebted to the inhabitants and owners who gave access to their proprieties. A total of 106 locations and at least as many stakeholders were involved in this project.

BiodiverCity was funded by the Swiss National Science Foundation as a project of NRP54 'Sustainable development of the built environment'.

I most warmly thank my parents Ebi and Monika, my sister Charlotte, the 'Lehmann-family' and all my friends for the continuous support and friendship before, throughout and now after the PhD. Meta, I thank you for our relationship, for your manifold support, for the moments shared and for your understanding for the time we could not share. I am so much looking forward to our 'small mammal project'!

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname:	**Sattler Thomas**
Matrikelnummer:	**97-054-068**
Studiengang:	**Phil.-nat. Biologie**
	Bachelor ☐ Master ☐ Dissertation ☒
Titel der Arbeit:	**Biodiversity in urban landscape matrices: from species richness to functional community structure**
Leiter der Arbeit:	**Prof. Dr. R. Arlettaz** **Dr. F. Bontadina** **Prof. Dr. P. Duelli** **Dr. M. Moretti** **Dr. M. K. Obrist**

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

…………………………………………………………….

Ort/Datum

……………………………………………………………..

Unterschrift

Curriculum Vitae

Name: Thomas Lukas Sattler
Birthdate: 16th of March 1975 in Grenchen, Switzerland
Nation: Swiss citizen
Address: Holzwiesweg 46
8047 Zürich, Switzerland
Phone: +41 43 321 97 05
Mobile: +41 79 585 93 00
Email: thomassattler@gmx.net

Education

2006-2009	PhD Student within the NFP54 project "BiodiverCity" at the Swiss Federal Research Institute WSL and the department of Conservation Biology, University of Berne, Switzerland
2008	Scientific visit (1 month) to Spatial Ecology group of P. Legendre, Université de Montréal, Canada
2004-2005	Postgraduate course in Geographic Information Systems (GIS), University of Applied Sciences Rapperswil, Switzerland
2002-2003	Master Degree in Biology from the University of Berne, Department of Conservation Biology. Thesis on ecological factors and distribution of two bat species in Switzerland.
2000-2001	University exchange year in Caracas, Venezuela
1997-2002	Study of Biology at the University of Basel, minor subject: Environmental Studies
1993	High school exchange year in Brisbane, Australia
1988-1996	Secondary school in Solothurn, Switzerland

Work experience

Regular

2005	Employed by SWILD (www.swild.ch), Zürich, privately owned research centre for urban ecology and wild animal research (7 months): Environmental impact analysis: Influence of wind mills on bats; various GIS-projects – depiction of scientific results
2005	Practical training (3 months) and subsequent temporary employment (2 months) with the Central Secretariat of Pro Natura, Basel: Communication of new approaches in species conservation
2003-2004	SOPRANO PIPISTRELLE project, sponsored by the Swiss Bat Foundation and the University of Berne: Scientific and implementation work (Public relations & Education)
2004	Internship at the Swiss Ornithological Institute: Winter ecology of the Capercaillie (1 month)
1996-1997	Work as a gardener in Bern (7 months)

Part time and voluntary services

Since 2005	Board member of the ALA, the Society for Ornithology and Bird Conservation of Switzerland
2002-2008	Involvement in the "Monitoring of common breeding birds", Swiss Ornithological Institute, Sempach
1994-2008	Regional Director, coach and trainer for the exchange organisation Youth for Understanding (YFU)
99/01/02	Realization of three student projects on the topics "Bats" and "The relationship between man and animal"
2001	Research project on the jaguar, Los Llanos, Venezuela (2 months)
1997-1999	Leading role in the Pro Natura – WWF youth group for the conservation of nature, Basel.
93/97/98	Sea turtle protection projects on Crete/Greece and in Australia

Awards

VOLZ prize 2008 of the University of Berne (best paper out of a Master thesis)

Peer-reviewed publications & Thesis

Sattler T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M.K. Obrist and M. Moretti. In Prep. Arthropod and bird communities in cities: shaped by environmental control and high stochasticity.

Sattler T., M.K. Obrist, R. Arlettaz, M. Moretti and F. Bontadina. In Prep. Bat's exploitation of cities: the importance of spatial and environmental variables.

Fontana S., T. Sattler, F. Bontadina and M. Moretti. Submitted. How to manage the urban green to enhance bird species richness and diversity. Biological Conservation.

Sattler T., P. Duelli, M.K. Obrist, R. Arlettaz and M. Moretti. In review. Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecology.

Vandewalle M., F. de Bello, M. P. Berg, T. Bolger, S. Dolédec, F. Dubs, C. K. Feld, R. Harrington, P. A. Harrison, S. Lavorel, P. Martins da Silva, M. Moretti, J. Niemelä, P. Santos, T. Sattler, J. P. Sousa, M. T. Sykes, A. J. Vanbergen and B. A. Woodcock. In review. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodiversity and Conservation.

2009 Keller V. and T. Sattler. 2009. Themenheft Kiebitz (Editorial in German). Der Ornithologische Beobachter. 106: 261 – 262.

Sattler T., E. Rey and H. Schmid. 2009. Distribution and population development of the Northern Lapwing *Vanellus vanellus* in Switzerland 2005-2008 – Verbreitung und Populationsentwicklung des Kiebitzes *Vanellus vanellus* in der Schweiz 2005-2008. (in German with English summary). Der Ornithologische Beobachter. 106: 263 – 274.

Müller W., Ch. Glauser, T. Sattler and L. Schifferli. 2009. The effect of measures for the Northern Lapwing Vanellus vanellus in Switzerland and recommendations for its conservation – Wirkung von Massnahmen für den Kiebitz *Vanellus vanellus* in der Schweiz und Empfehlungen für die Artenförderung (in German with English summary). Der Ornithologische Beobachter. 106: 327 – 350.

2008 Kouakou D., T. Sattler, M.K. Obrist, P. Duelli and M. Moretti. 2008. Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft. 81 (3/4). 191-198.

	Germann Ch., T. Sattler, M.K. Obrist and M. Moretti. 2008. Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). Mitteilungen der Schweizerischen Entomologischen Gesellschaft. 81 (3/4): 141-154.
2007	Sattler T., F. Bontadina, A. Hirzel and R. Arlettaz. 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. Journal of Applied Ecology, 44, 1188-1199.
2004	Sattler T. and M. Tobler. 2004. Development of breeding populations of birds in two residential areas in Solothurn and their dependence on habitat structure – Bestandsentwicklung und Strukturabhängigkeit von Brutvögeln in zwei Wohnquartieren der Stadt Solothurn (in German with English summary). Der Ornithologische Beobachter 101 (3): 177-192.
2003	Sattler T. 2003. Ecological factors affecting the distribution of the sibling species *Pipistrellus pygmaeus* and *Pipistrellus pipistrellus* in Switzerland. Master thesis, University of Berne, Berne.

Applied publications

2008	Sattler, T., S. Ashrafi, F. Bontadina. 2008. Langzeit-Monitorings sind möglich. Fledermaus-Anzeiger 87: 5.
2006	Bontadina, F. und T. Sattler. 2006. Windenergie in Deutschland und Frankreich: Sorgen wegen Fledermäusen – und die Lösungssuche. Fledermaus-Anzeiger 83: 1-3.
2005	Sattler, T. und F. Bontadina. 2005. Grundlagen zur ökologischen Bewertung von zwei Windkraftgebieten in Frankreich aufgrund der Diversität und Aktivität von Fledermäusen. Kurzbericht. SWILD, Zürich im Auftrag von Megawatt Eole, Stuttgart, 23 Seiten.
2004	Sattler, T. 2004. Ein Winzling unter Zwergen. Ornis 2/04: 38-39.
2003	Sattler, T. und F. Bontadina. 2003. Wo lebt die Mückenfledermaus in der Schweiz? Fledermaus-Anzeiger 75: 4-5.
2002	Sattler, T. und F. Bontadina. 2002. Die Mückenfledermaus – erstmaliger Fortpflanzungsnach-weis, Fledermaus-Anzeiger 72: 1-2.

Oral presentations at conferences and invited seminars

2009	Thomas Sattler, P. Duelli, M.K. Obrist, F. Bontadina, R. Arlettaz, M. Moretti. Analysis of urban arthropod communities on different spatial scales reveal ecological information hidden by robust species richness measures. European Congress for Conservation Biology, Prague, Sept. 1-5 2009.
	Sattler, T. Urban arthropods: Surprisingly high robustness of species richness. Seminar at the Department of Ecology and Evolution, University of Lausanne. May 19 2009
2008	Sattler, T., M. Ruedi, P. Zingg, M.K. Obrist and F. Bontadina. 2008. Red list status determined by area of distribution: a case study on *Pipistrellus pygmaeus*. XIth European Bat Research Symposium, Cluj-Napoca, Romania. Aug. 18-22 2008.
	Sattler, T., P. Duelli, M.K. Obrist, F. Bontadina, R. Arlettaz, M. Moretti. 2008. The influence of past and present human decisions on urban arthropod diversity. Urban Biodiversity & Design. International Conference Erfurt, Germany. May 21-24 2008.
2006	Sattler, T., Schorcht, W., Hirzel, A., R. Arlettaz and F. Bontadina. 2006. GIS habitat suitability models identify species-specific bat hotspots: from home range to landscape scale. Bat Conservation Trust, National Bat Conference U.K. University of Reading, Sept. 22-24 2006.
2005	Sattler, T., Beck, A., Eicher, C., Hotz, T., Märki, K., Lutz, M., Mühlethaler E. and F. Bontadina. 2005. Projekt Rhippos – Von Telemetriedaten zu Jagdgebieten einer Fledermaus-kolonie: eine GIS-Extrapolation. Nationale Fledermaus-Tagung. Berne, Switzerland. Nov. 5 2005.
	Sattler, T., Schorcht, W., Bontadina, F. 2005. From radio-tracking data of individual bats to foraging areas of a bat colony: extrapolation using Ecological Niche Factor Analysis (ENFA). Galway, Ireland. Tenth European Bat Research symposium, Aug. 21-26 2005.
2003	Sattler T., Bontadina, F., Arlettaz, R. 2003. Ecological factors affecting the distribution of the sibling bat species *Pipistrellus pygmaeus* and *Pipistrellus pipistrellus* in Switzerland. 23. Jahresversammlung Schweizerische Gesellschaft für Wildtierbiologie. Berne, Sept. 21-25 2003.

Posters

2008	Moretti M., T. Sattler, R. Home, F. Bontadina, N. Bauer, S. Gloor, P. Duelli, P. Della Bruna, M.K. Obrist, M. Hunziker. 2008. BiodiverCity – Ecological and social value of urban nature. How to maintain and improve biodiversity and its acceptance in urban areas. Urban Biodiversity & Design. International Conference Erfurt, Germany. May 21-24 2008.
2007	Sattler, T., Duelli, P., Obrist, M.K., Bontadina, F., Arlettaz, R., Moretti, M. 2007. Increased human management negatively affects beetle (Coleoptera) richness in Swiss cities. International Association of Landscape Ecology, World Congress, Wageningen. July 9-12 2007.
2004	Sattler T., Bontadina, F., Arlettaz, R. 2004. From scientific results to a conservation strategy: The case of the Soprano Pipistrelle Bat (Pipistrellus pygmaeus) in Switzerland. Student Conference on Conservation Science, University of Cambridge, March 24-26 2004.
2003	Sattler T., Bontadina, F., Arlettaz, R. 2003. Ecological factors affecting the distribution of the sibling bat species Pipistrellus pygmaeus and Pipistrellus pipistrellus in Switzerland. Student Conference on Conservation Science, University of Cambridge, March 26-28 2003.