The impacts of urbanisation and habitat size on local biodiversity and ecosystem functioning

Inauguraldissertation

zur Erlangung der Würde eines Doktors der Philosophie

vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von

Ramona Laila Melliger
aus Sarmenstorf AG

Basel, 2019

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät
auf Antrag von

Prof. Dr. Bruno Baur

Prof. Dr. Yvonne Willi

Basel, den 19. September 2017

Prof. Dr. Martin Spiess
Dekan

ACKNOWLEDGEMENTS

First and foremost, I am deeply thankful to Prof. Bruno Baur for giving me the opportunity to conduct my PhD in his research group at the University of Basel. With his guidance, valuable scientific advice, useful critique and fast and helpful feedback on my manuscripts, he contributed greatly to my thesis.

I would like to express my deep gratitude to my supervisor Hans-Peter Rusterholz for his comprehensive support and endless patience. I am grateful for the great amount of time he spent for introducing me into lab work and assisting me with statistics. I am also thankful for his valuable advices during field work preparation, his helpful comments on my manuscripts, and his support and nice company during some field and lab work days.

I would like to express my deep gratitude also to Brigitte Braschler for her statistical advices. In particular, I am thankful for her contribution, expertise and support during the whole implementation process of the last manuscript (Chapter II), especially the identification of ants and the acquisition of funds for the sorting of pitfall traps.

My special thanks are extended to my co-referent Prof. Yvonne Willi, who kindly accepted to be a member of my thesis committee.

I would like to greatly thank Ambros Hänggi for introducing me in the identification of spiders and for verifying and identifying some part of the spider samples.

The next thanks go to all people from the NLU – current and former – for the nice company and their willingness to help in every occasion. In particular, I would like to express my very great appreciation to Eliane Riedener for her support and nice company throughout my master. The collaboration with her and her helpful advices prepared me very well for writing my doctoral thesis. I am grateful to Anette Baur and Brigitte Braschler for their valuable comments on the manuscripts. I further thank Denise Binggeli, Luca Gaggini, Julie Hart, Dominik Milner, Kai Reinacher, Roman Schneider, Hanrong Tan, Fabian Toscan for their assistance in analysing the litter and soil characteristics and/or sorting the pitfall-trap content.

I wish to thank various people outside the NLU for their contribution to my work: The foresters, Christoph Merian Stiftung, Industrielle Werke Basel, Stadtgärtnerei Basel and private owners for access to the study sites and Rainer Neumeyer and Bernhard Seifert for the verifications of ant identification of some ant specimen. A special thank goes to Yvonne Reisner from the Stadtgärtnerei Basel for the provision of the data of the inventory and comprehensive answers to questions regarding it. In this context, I also thank Claudia Farrèr for introducing me in the handling of databases.

Financial support was received from the Stadtgärtnerei Basel, Emilia Guggenheim-Schnur Stiftung and Basler Stiftung für Biologische Forschung.

Finally, I would like to greatly thank my family and close friends for their encouragement and endless patience, especially my best friend and former flat mate Janine Wüthrich. Last but not least, a want to say a huge “Merci vell mol” to my dearly parents, Sepp and Luzia Melliger, for their endless love, support and trust in me and my abilities throughout my life.

CONTENTS

SUMMARY

Urbanisation is increasing worldwide and regarded a main driver of environmental change. Urban development and associated factors like increased spatial isolation, reduced habitat size and various types of disturbances can alter the dynamics of plant and animal populations in the remaining green areas. Furthermore, changes in abiotic site conditions (e.g. temperature, moisture content) can influence habitat quality and, consequently, the species richness, species composition and functional diversity of plants and animals, which in turn can affect the functioning of ecosystems. Nonetheless, urban areas can harbour a remarkably high species richness and can be of high conservation value by serving as a refugia for many rare and threatened species. It is, therefore, of central importance in conservation biology to disentangle the various drivers of biodiversity in urban landscapes. Within the scope of this thesis, three studies were conducted to examine the consequences of urbanisation on the biodiversity and ecosystem functioning of green areas in the urban region of Basel, Switzerland.

The aim of the first study was to assess the impacts of habitat size and landscape composition of the closer surroundings on the species diversity of three taxonomic groups differing in trophic rank (vascular plants, Orthoptera and Lepidoptera) in meadows and ruderal sites. I also related the response of three traits (body size, dispersal ability and food specialisation) to habitat size in Orthoptera and Lepidoptera. For this purpose, I analysed data of species from the natural heritage inventory of Basel. I found that the response of different groups of species considerably varied depending on the habitat type, taxonomic group and species trait examined. The species richness of Orthoptera and Lepidoptera was positively related to meadow size but not to the size of ruderal sites, while the opposite was true for plants. For Lepidoptera in ruderal sites, the percentage of ruderal sites in the closer surroundings was a better predictor of species richness than habitat size per se.

Forests belong to the most frequent green areas in urban landscapes and provide a wide range of ecosystem functions and thus play a major role for human well-being in cities. The aim of the second study was to examine the potential effects of degree of urbanisation, forest size and the corresponding interaction on the species diversity and functional diversity of vascular plants, ants and spiders. The two arthropod groups do not show species-specific mutualistic or exploitative relationships with plants in contrast to those in the first study. I conducted vegetation surveys and pitfall trapping to sample soil surface-active ants and spiders. In plants, species richness decreased with the degree of urbanisation. Ants and spiders at higher trophic rank showed more pronounced shifts in species composition with increasing degree of urbanisation, while the percentage of forest specialists in both arthropod groups was positively related to forest size. Local site characteristics were also important determinants for species diversity and functional diversity.

In forests, the decomposition of leaf litter is an important component of the process of nutrient cycling and the formation of soil. In this way, litter decomposition contributes to the maintenance of several other ecosystem functions and services. The third study aimed to investigate the effects of urbanisation on leaf litter decomposition process in forests. Standardised litter of *Fagus sylvatica* leaves was used to assess the impact of urbanisation-related factors on the early stage of decomposition and seasonal microbial activity. I found combined effects of degree of urbanisation and forest size on the decomposition rate of leaf litter (k_{litter}) indicating that forests of similar size differed in abiotic and biotic forest characteristics depending on the degree of urbanisation in the closer surroundings. Furthermore, moisture content of litter was the best predictor of microbial activity, followed by forest size.

The findings of this thesis highlight the necessity to consider different taxonomic groups and functional groups in urban planning to maximise conservation value of urban green areas. In addition to degree of urbanisation, also habitat size was important for the diversity of some groups and leaf litter decomposition process in forests. It was also encouraging to find that even small green sites have the potential to make a significant contribution to biodiversity conservation and essential ecosystem functions in urban landscapes. I recommend that urban planners develop more flexible management strategies to satisfy the different requirements of various groups of species in the corresponding habitat type. Locally adapted management practices may provide a way forward to enhance habitat quality in a way to maximise species diversity and thus ensure the functioning of ecosystems; albeit large-scale factors also remain important.

GENERAL INTRODUCTION

Urbanisation is increasing globally. By the year 2050, 66% of the world's population is predicted to live in cities (United Nations 2014) with the consequence that the pressure on the remaining urban green sites will increase. This is of concern as urbanisation is considered to be a major driver of environmental change (Grimm et al. 2008). Several studies reported an increase in temperature, precipitation and N deposition from the rural surroundings to the city centre (Grimm et al. 2008; Pickett et al. 2011). Furthermore, urban development and associated factors like increased spatial isolation, reduced habitat size and various types of disturbances can alter the dynamics of plant and animal populations in the remaining green areas (Niemelä 1999; McKinney 2002). These changes influence habitat quality and, consequently, the diversity of species and functional traits (Sukopp 1998; McKinney 2002; Concepción et al. 2015), which in turn can affect the functioning of ecosystems (Chapin et al. 1997).

Nonetheless, urban areas can harbour a remarkably high species richness, in some cases exceeding that of their rural surroundings (Sukopp 1998; Deutschewitz et al. 2003; Kühn et al. 2004). Explanations for the high species richness include additions to the regional species pool such as non-native species or species adapted to urban habitats without a natural analogue in rural surroundings. The pronounced habitat heterogeneity on a small spatial scale typical for urban landscapes results in a mosaic of various habitat types ranging from semi-natural to highly modified ones, some of them unique to urban landscapes (e.g. Rebele 1994; Niemelä 1999; Wania et al. 2006). Consequently, edge effects play an important role with generalist species and species from neighbouring habitat types immigrating into small habitat patches. It is, therefore, of central importance in conservation biology to disentangle the various drivers of biodiversity in urban landscapes (McKinney 2002; Kowarik 2011). In addition to high species richness, green areas in cities such as meadows, ruderal sites and forests can serve as refugia for numerous rare and threatened species and thus can be of high conservation value (Niemelä 1999; Muratet et al. 2007; Öckinger et al. 2009; Albrecht and Haider 2013). However, these habitat types differ substantially in abiotic factors, site history, management and disturbance intensity (Kowarik 2011) and thus in species composition.

Not all species respond to environmental changes caused by urbanisation in the same way, because they have different requirements regarding their habitat and its surrounding landscape (McIntyre et al. 2001; Concepción et al. 2015). For example, groups of species at high trophic ranks such as herbivores and predators are often more strongly affected by spatial isolation and habitat loss due to their dependence on other species than groups of species at low trophic ranks such as plants (Holt et al. 1999; Steffan-Dewenter 2003). Species more sensitive to spatial isolation and habitat loss were also found to share particular life-history traits such as large body size, low dispersal ability and high food and habitat specialisation (e.g. McKinney and

Lockwood 1999; Tscharntke et al. 2002; Magura et al. 2010; Öckinger et al. 2010; Lizée et al. 2011a).

Focus of the thesis

The main aim of this thesis is to examine the consequences of urbanisation on the biodiversity and ecosystem functioning of green areas in the canton Basel-Stadt (comprising the city of Basel and the municipalities Riehen and Bettingen), Switzerland. To address this question, I used species inventories of meadows and ruderal sites (Chapter I) and conducted field surveys and experiments in forest sites (Chapter II and III). In the study area, the green sites examined were very small and embedded in a small-scattered landscape, where settlements and green areas were located within short distances. An urban–rural gradient approach extending over several kilometres was, therefore, not appropriate in our study area. Instead, I used the percentage cover of sealed area in the closer surroundings as a measure of spatial isolation and degree of urbanisation.

Previous studies addressed the consequences of urban sprawl for diverse organisms (e.g. Magura et al. 2004; McKinney 2008; Vallet et al. 2010; Nufio et al. 2011; Vergnes 2014). Nonetheless, most of these studies focused on only one single taxon or on taxonomic groups at similar trophic rank in one habitat type, whereas multi-taxa studies examining the effect of urbanisation on biodiversity at both the species and trait level are still rare (for exceptions see Lizée et al. 2011a; Concepción et la. 2016). This is of particular importance, as management actions that support the diversity of one taxonomic group or promote one species can be inappropriate or even detrimental for other groups of species. Therefore, to support a wide range of biodiversity, conservation strategies should be developed based on studies of more than one group of species.

In the years 2008 and 2009, field surveys considering different taxonomic groups and habitat types were conducted by the Stadtgärtnerei Basel in the canton Basel-Stadt to identify green areas of high conservation value (Reisner et al. 2013). In **Chapter I,** I present the results of statistical analyses of this inventory, which aimed to assess the impacts of habitat size and landscape composition in the closer surroundings on the species richness and trait diversity of vascular plants, Orthoptera and diurnal Lepidoptera in meadows and ruderal sites. The three taxonomic groups differ in trophic rank and thus in the use of resources available in the urban landscape. Furthermore, species that inhabit meadows and ruderal sites differ in species attributes and thus may respond to changes in habitat size and the surrounding landscape in different ways (Öckinger et al. 2009; Lizée et al. 2011b).

A main focus of my thesis is on urban forests. I examined both the biodiversity of these forests as well as the impact of urbanisation on an important ecosystem process, namely leaf litter decomposition. Forests represent the most frequent type of green area in the study region (1.7 km^2 resp. 11.7%; Statistisches Amt Kanton Basel-Stadt 2017). Urban forests provide a wide range of ecosystem functions and services, from habitat for native species to the recycling and storage of nutrients, air filtering, temperature regulation and recreation to residents (Dwyer et al. 1992; Bolund and Hunhammer 1999; Berg and McClaugherty 2014) and thus play a major role for human well-being in cities. **Chapter II** presents the results of a field survey, which investigated the potential effects of degree of urbanisation and forest size and the corresponding interaction on the species diversity and functional diversity of vascular plants, soil-surface active ants and spiders. As in Chapter I, the taxonomic groups considered differed in trophic rank and thus in the use of resources available. However, neither of the two arthropod groups depend on specific plant species as food resource, in contrast to the Orthoptera and Lepidoptera examined in Chapter I. Ants use some plant products directly but can obtain them from many different species. In contrast, spiders only indirectly depend on plants. Hence, the responses of ants and spiders to urbanisation can be expected to be independent of that of plants.

In forests, the decomposition of leaf litter is an important component of the process of nutrient cycling and the formation of soil. It mineralises nutrients into forms accessible for plants and is the basis of soil formation (Swift et al. 1979; McDonnell et al. 1997; Berg and McClaugherty 2014). In this way, litter decomposition contributes to the maintenance of several other ecosystem functions and services. Most urban studies on decomposition processes were conducted in North America. In Europe, urban studies on leaf decomposition are restricted to *Quercus ilex* in Mediterranean forests (Cotrufo et al. 1995) and *Populus tremula* in boreal forests (Nikula et al. 2010). The European beech (*Fagus sylvatica* L.) is one of the most frequent deciduous tree species in temperate forests in Central Europe (Bolte et al. 2007). So far, however, effects of urbanisation on the decomposition processes of *F. sylvatica* leaves have not been examined. **Chapter III** presents the results of a field survey, which used standardised litterbags with leaves of *F. sylvatica* to assess the impact of urbanisation-related factors on the early stage of decomposition and seasonal microbial activity. In this survey, I exposed litterbags in forest of different size for periods of different lengths.

In the final section of this thesis, the **General Discussion**, I discuss the most important findings of the three chapters and their implications for the management of green areas in the urban region of Basel.

References

Albrecht H., Haider S., 2013. Species diversity and life history traits in calcareous grasslands vary along an urbanization gradient. Biodivers. Conserv. 22: 2243–2267.

Berg B., McClaugherty C., 2014. Plant litter: decomposition, humus formation, carbon sequestration, 2nd ed. Springer, Heidelberg.

Bolte A., Czajkowski T., Kompa T., 2007. The north-eastern distribution range of European beech – a review. Forestry 80: 413–429.

Bolund P., Hunhammer S., 1999. Ecosystem services in urban areas. Ecol. Econ. 29: 293–301.

Chapin F.S., Walker B.H., Hobbs R.J., Hooper D.U., Lawton J.H., Sala O.E., Tilman D., 1997. Biotic control over the functioning of ecosystems. Science 277: 500–504.

Concepción E.D., Moretti M., Altermatt F., Nobis M.P., Obrist M.K., 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos 124: 1571–1582.

Concepción E.D., Obrist M.K., Moretti M., Altermatt F., Baur B., Nobis M.P., 2016. Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosyst. 19: 225–242.

Cotrufo M.F., DeSanto A.V., Alfani A., Bartoli G., DeCristofaro A., 1995. Effects of urban heavy metal pollution on organic matter decomposition in *Quercus ilex* L. woods. Environ. Pollut. 89: 81–87.

Deutschewitz K., Lausch A., Kühn I., Klotz S., 2003. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Glob. Ecol. Biogeogr. 12: 299–311.

Dwyer J.F., McPherson E.G., Schroeder H.W., Rowntree R., 1992. Assessing the benefits and costs of the urban forest. J. Arboric. 18: 227–234.

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

Holt R.D., Lawton J.H., Polis G.A., Martinez N.D., 1999. Trophic rank and the species–area relationship. Ecology 80: 1495–1504.

Kowarik I., 2011. Novel urban ecosystems, biodiversity, and conservation. Environ. Pollut. 159: 1974–1983.

Kühn I., Brandl R., Klotz S., 2004. The flora of German cities is naturally species rich. Evol. Ecol. Res. 6: 749–764.

Lizée M.H., Bonardo R., Mauffrey J.F., Bertaudière-Montes V., Tatoni T., Deschamps-Cottin M. 2011a. Relative importance of habitat and landscape scales on butterfly communities of urbanizing areas. C. R. Biol. 334: 74–84.

Lizée M.H., Mauffrey J.F., Tatoni T., Deschamps-Cottin M., 2011b. Monitoring urban environments on the basis of biological traits. Ecol. Indic. 11: 353–361.

Magura T., Tóthmérész B., Molnár T., 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecol. 19: 747–759.

Magura T., Horváth R., Tóthmérész B., 2010. Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary. Landscape Ecol. 25: 621–629.

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

McDonnell M.J., Pickett S.T.A, Groffman P., Bohlen P., Pouyat R.V., Zipperer W.C., Parmelee R.W., Carreiro M.M., Medley K., 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosyst. 1: 21–36.

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

McKinney M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. – Urban Ecosyst. 11:161–176.

McKinney M.L., Lockwood J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14: 450–453.

Muratet A., Machon N., Jiguet F., Moret J., Porcher E., 2007. The role of urban structures in the distribution of wasteland flora in the greater Paris area, France. Ecosystems 10: 661–671.

Niemelä J., 1999. Ecology and urban planning. Biodivers. Conserv. 8: 119–131.

Nikula S., Vapaavouri E., Manninen S., 2010. Urbanization-related changes in European aspen (*Populus tremula* L.): Leaf traits and litter decomposition. Environ. Pollut. 158: 2132–2142.

Nufio C.R., McClenahan J.L., Bowers M.D., 2011. Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. J. Insect Conserv. 15: 409–419.

Öckinger E., Dannestam A., Smith H.G., 2009. The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landsc. Urban Plan. 93: 31–37.

Öckinger E., Schweiger O., Crist T.O., Debinski D.M., Krauss J., Kuussaari M., Petersen J.D., Pöyry J., Settele J., Summerville K.S., Bommarco R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13: 969–979.

Pickett S.T.A., Cadenasso M.L., Grove J.M., Boone C.G., Groffman P.M., Irwin E., Kaushal S.S., Marshall V., McGrath B.P., Nilon C.H., Pouyat R.V., Szlavecz K., Troy A., Warren P., 2011. Urban ecological systems: scientific foundations and a decade of progress. J. Environ. Manage. 92: 331–362.

Rebele F., 1994. Urban ecology and special features of urban ecosystems. Glob. Ecol. Biogeogr. 4: 173–187.

Reisner Y., Plattner M., Berney C., Birrer S., Farrèr C., Frei M., Küry D., Ramseier P., Steck C., Zemp M., 2013. Unbekannte Schätze vor der Haustür – Ergebnisse des Naturinventars im Kanton Basel-Stadt. Bau- und Verkehrsdepartement des Kanton Basel-Stadt, Stadtgärtnerei, Basel.

Statistisches Amt Kanton Basel-Stadt. 2017. Tabellen: Bevölkerung; Bodennutzung; Pendler. <http://www.statistik.bs.ch/zahlen/tabellen. html>. Accessed 27 February 2017.

Steffan-Dewenter I., 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv. Biol. 17: 1036–1044.

Sukopp H., 1998. Urban ecology: scientific and practical aspects. In: Breuste, J., Feldmann, H., Uhlmann, O. (Eds.), Urban Ecology. Springer Verlag, Berlin, pp. 3–16.

Swift M.J., Heal O.W., Anderson J.M., 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, CA.

Tscharntke T., Steffan-Dewenter I., Kruess A., Thies C., 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecol. Res. 17: 229–239.

(UN) United Nations. 2014. World urbanization prospects, the 2014 revision. <http://esa.un.og/unpd/wup>. Accessed 26 May 2016.

Vallet, J., Beaujouan V., Pithon J., Rozé F., Daniel H., 2010. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. Biodivers. Conserv. 19: 3375–3392.

Vergnes A., Pellissier V., Lemperiere G., Rollard C., Clergeau P., 2014. Urban densification causes the decline of ground-dwelling arthropods. Biodivers. Conserv. 23: 1859–1877.

Wania A., Kühn I., Klotz S., 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. Landsc. Urban Plan. 75: 97–110.

Chapter I

Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape

Ramona L. Melliger, Hans-Peter Rusterholz, Bruno Baur

Urban Ecosystems, 2017, 20: 1095–1107

Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape

Ramona Laila Melliger, Hans-Peter Rusterholz, Bruno Baur

Section of Conservation Biology, Department of Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

Abstract

Urban growth is considered to be a major driver of environmental change. Urbanisation can affect urban biodiversity in different ways. So far, most studies focused on the impact of urbanisation on single taxa in one habitat type. In this study, we used data of species inventories and GIS-based landscape elements to examine the effects of habitat size and landscape composition on the species diversity of three taxonomic groups (vascular plants, Orthoptera and Lepidoptera) in meadows and ruderal sites in the urban region of Basel, Switzerland. We also related the responses of three species traits (body size, dispersal ability and food specialisation) to habitat size in Orthoptera and Lepidoptera. We found that species of the different taxonomic groups differed in their response to habitat size and landscape composition both in meadows and ruderal sites depending on the traits examined. The species richness of Orthoptera and Lepidoptera was positively related to meadow size but not to the size of ruderal sites, while the opposite was true for plants. For Lepidoptera in ruderal sites, the percentage cover of ruderal area in the closer surroundings was a better predictor of species richness than habitat size per se. To sustain high levels of urban biodiversity, we recommend that urban planners develop adequate management strategies to satisfy the different requirements of various taxonomic groups and to increase the quality of green sites surrounding the target habitat.

Keywords urbanisation • species–area relationship • grasshoppers • butterflies • plant functional richness

Introduction

Urban growth is considered to be a major driver of environmental change (Grimm et al. 2008). Urbanisation can affect both the diversity and composition of plants and animals by various factors including reduced habitat size, changed habitat quality, spatial isolation and different types of disturbances (e.g. Blair and Launer 1997; McKinney 2002; Knapp et al. 2008; Concepción et al. 2016). Nonetheless, urban areas can harbour a remarkably high species richness (Deutschewitz et al. 2003; Godefroid and Koedam 2007), in some cases exceeding that of their rural surroundings (Kühn et al. 2004; Wania et al. 2006). Explanations for the high species richness are the spread of generalist and non-native species and the pronounced habitat heterogeneity on a small spatial scale resulting in a mosaic of various habitat types ranging from semi-natural to highly modified ones, some of them unique to urban landscapes (e.g. Rebele 1994; Pyšek 1998; Niemelä 1999; Wania et al. 2006; Germann et al. 2008; Sattler et al. 2010). A central issue in conservation biology is to disentangle the various factors that influence urban biodiversity (McKinney 2002; Kowarik 2011).

Meadows and ruderal sites can have a high species richness and conservation value in urban areas (Öckinger et al. 2009; Fischer et al. 2013). These habitat types provide refuges for numerous rare and threatened species, whose primordial habitats have decreased in the past decades (Öckinger et al. 2006; Muratet et al. 2007; Albrecht and Haider 2013). However, meadows and ruderal sites differ substantially in abiotic factors, site history, management and disturbance intensity (Kowarik 2011) and thus in species composition. Within city areas, meadows are often remnants of former large continuous grasslands. Nowadays, these meadows are frequently mown and thus exposed to a moderate level of disturbance. In contrast, ruderal sites such as vacant lands, little used or unused railway tracks and marshalling yards are irregularly but intensively disturbed habitats (Wittig 2002). Many ruderal sites constitute short-lived habitats as they become destroyed by overbuilding. In the absence of disturbance they may become overgrown by ongoing succession (Wittig 2002; Muratet et al. 2007; Müller et al. 2013).

As a consequence of proceeding urban development, meadows and ruderal sites decrease in area and become more isolated, which in turn may lead to the local extinction of species (MacArthur and Wilson 1967; Muratet et al. 2007). However, the response to reduced habitat size varies among groups of organisms that differ in trophic rank and life-history traits. Groups of species at high trophic ranks such as herbivores and predators are often more strongly affected by habitat loss due to their dependence on other species than groups of species at low trophic ranks such as plants (Steffan-Dewenter and Tscharntke 2000; Steffan-Dewenter 2003; van Noordwijk et al. 2015). Species more sensitive to habitat loss were also found to share particular life-history traits such as large body size, low dispersal ability and high food and habitat specialisation (e.g. McKinney and Lockwood 1999; Tscharntke et al. 2002; Öckinger et al. 2010; Lizée et al. 2011a; Nufio et al. 2011).

Previous studies showed that the composition of the surrounding landscape can play an important role for species' persistence in fragmented landscape as well, because it can mitigate or intensify the consequences of habitat loss and spatial isolation (Steffan-Dewenter 2003; Godefroid and Koedam 2007; Barbaro and van Halder 2009; Sattler et al. 2010; Lizée et al. 2012; Öckinger et al. 2012a,b). For example, species of plant hoppers and butterflies can use existing green areas in the surroundings as corridors to move among habitat patches (Ricketts 2001; Baum et al. 2004) or benefit from additional resources outside the focal habitat patch (Dunning et al. 1992).

As different groups of species have different requirements on their habitat and its surrounding matrix, management actions that support the diversity of one taxonomic group or species can be inappropriate or even detrimental for other groups or species. Therefore, to support a wide range of urban biodiversity, conservation strategies should be developed on findings of more than one species group. Some studies applied multi-species approaches to identify those species groups that suffer most from proceeding urbanisation and to describe the mechanisms that lead to the selective loss of species (e.g. Kattwinkel et al. 2009; Sattler et al. 2010; Lizée et al. 2011b; Nufio et al. 2011; Soga et al. 2014). So far, however, few studies have examined the impact of urbanisation on biodiversity at both the species and trait level (for exceptions see Lizée et al. 2011a; Concepción et al. 2016). The impact of urbanisation on biodiversity may also vary among different habitat types. Species that inhabit meadows and ruderal sites differ in species attributes and thus may respond to changes in habitat size and the surrounding landscape in different ways (Öckinger et al. 2009; Lizée et al. 2011b). Hence, findings on species' response to urbanisation are restricted to a particular habitat type and should not be extrapolated to other habitat types.

In this study, we examined the impact of habitat size and landscape composition in the closer surroundings on the species richness and trait diversity of vascular plants, Orthoptera and Lepidoptera in meadows and ruderal sites in Basel, Switzerland. Species data were obtained from the natural heritage inventory of Basel (Reisner et al. 2013). The groups examined vary in trophic rank and thus in the use of resources available in the urban landscape.

In particular, we tested the following hypotheses:

(1) Species richness of vascular plants, Orthoptera and Lepidoptera increase with increasing size of both meadows and ruderal sites. This effect is more pronounced in groups of higher trophic rank (Orthoptera, Lepidoptera) than in plants at a lower trophic rank (hypothesis of trophic rank-related species–area relationship).

(2) The percentage cover of sealed area in the closer surroundings of meadows and ruderal sites negatively affects species richness of all three taxonomic groups and plant functional richness. In contrast, the percentage cover of green areas (agricultural land, ruderal areas, urban green space, forests and water) in the closer surroundings differently influences both species richness and composition of the three target groups (surrounding landscape effect hypothesis).

(3) In Orthoptera and Lepidoptera, the numbers of species with a large body, high dispersal ability and high food specialisation increase with urban habitat size (area-related trait hypothesis).

Methods

Study area

The study was conducted in the canton of Basel-Stadt (hereafter referred to as Basel; Fig. 1), Switzerland (47°34'N, 7°36'E, elevation: 245–522 m a.s.l). The study area measures 37 km^2 and is predominately covered by residential areas (70.9%), agricultural land (12.1%) and forest (11.7%; Statistisches Amt Kanton Basel-Stadt; www.statistik-bs.ch, 2015). It includes the city of Basel and the two municipalities Bettingen and Riehen. Basel has 197'205 inhabitants (www.statistik-bs.ch, 2015) and a high number of people that commute for work from France and Germany (34'890) and other parts of Switzerland (62'880, www.statistik-bs.ch, 2015). Total annual precipitation averages 842 mm, with an annual mean temperature of 10.5 °C and average temperatures of 1.6 °C in January and 19.7 °C in July (records from 1982–2010; MeteoSwiss, 2016).

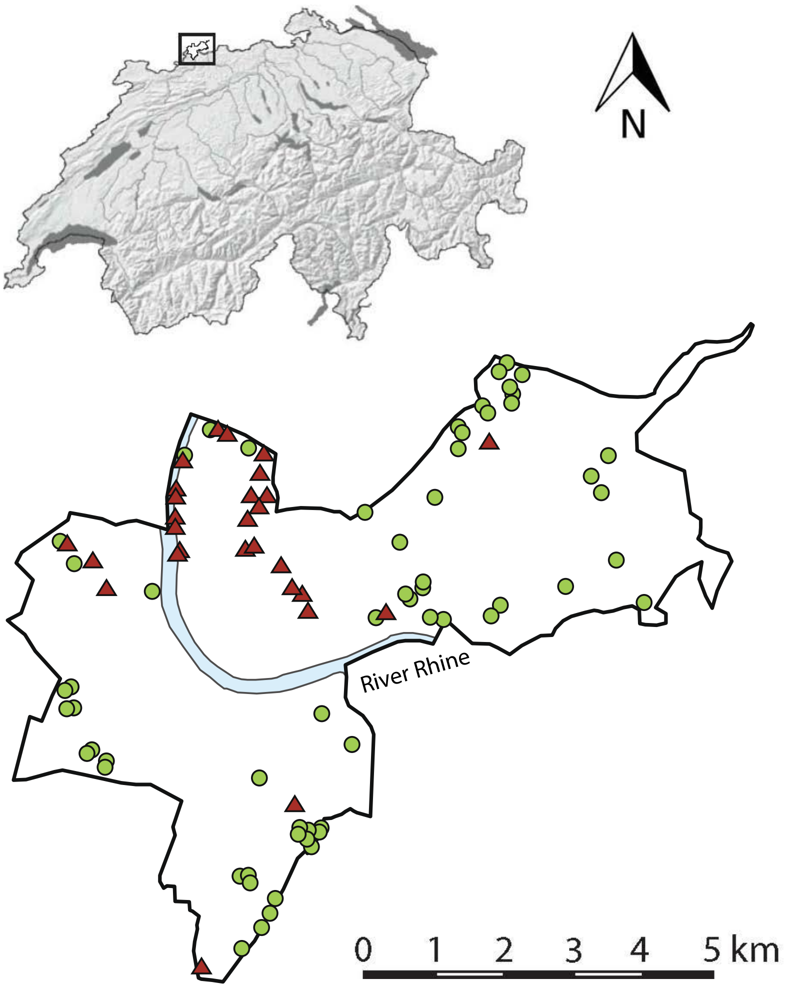


Fig. 1 Location of the study area in Northwestern Switzerland and the distribution of the meadows (circles) and ruderal sites (triangles) examined in the area of Basel. The investigation area is surrounded by dense settlements in Germany (north), France (northwest) and Switzerland (south-west)

Species data and sampling methods

We analysed presence–absence data of species from three taxonomic groups (vascular plants, Orthoptera, diurnal Lepidoptera) based on lists of the natural heritage inventory of Basel (Reisner et al. 2013). Species inventories were conducted by experienced botanists and zoologists in the years 2008 and 2009. We focused on two habitat types (Fig. 1): meadows and ruderal sites, as most of the habitat patches surveyed for Orthoptera (92%) and diurnal Lepidoptera (85%) belonged to either of these habitat types. The number of habitat patches investigated differed between the three groups of organisms, because the three inventories were conducted separately. The overlap between habitat sites of plants and Orthoptera was 88%, between plants and Lepidoptera 81% and between Orthoptera and Lepidoptera 78%. In 61% of the habitat sites all three taxonomic groups were considered.

The aim of the inventories was to record a maximum number of species in a habitat site. Therefore, the sampling designs differed with respect to the different phenology of the three groups of organisms. For vegetation surveys, meadows were visited once between May and June, whereas ruderal sites were sampled twice: once between April and May to account for plant species only detectable in spring and once between June and August to complete the plant lists. Plant species (including woody plants) were recorded by slowly walking in zig–zag lines over the entire habitat patch. Due to this procedure, sampling effort was proportional to patch size.

Transect methods were used to survey habitat patches for Orthoptera and Lepidoptera. Depending on the perimeter of the patches, the transect lines were arranged in linear or serpentine patterns, 5 m wide, in order to cover the entire area. The sampling effort was approximately proportional to the size of habitat patches. Invertebrate transects were only surveyed under good weather conditions (sunshine duration ≥ 80%, temperature 16–32 °C and wind-speed ≤ 16 km/h (Beaufort scale 3)) from 10 a.m to 6 p.m and for Orthoptera, additionally, from 9 p.m. to 11 p.m. Habitat patches of Orthoptera were optically and acoustically surveyed twice between July and August: once during the day and once in the evening to detect species highly vocal at dusk. A bat detector (SSF Fledermausdetektor) was used to locate species living in hidden places and stridulating with high frequencies like the long-winged conehead *Conocephalus discolor*. The Lepidoptera surveys were conducted once in spring from 20 April to 25 May and once in summer from 20 June to 25 July. All species of Rhopalocera, Hesperiidae and Zygaenida were recorded.

Landscape composition

To assess the landscape composition around each habitat patch, land cover types and landscape characteristics were derived from official geographic information systems (Geoportal Kanton Basel-Stadt 2014; Geo BL 2014; Geoportal Baden-Würrtemberg 2014). Within a radius of 200 m around the centre of each habitat patch, the percentage cover of sealed area (settlements, roads etc.), agricultural area (including meadows), ruderal area, urban green space (parks, gardens etc.), forest and water surface area were determined using ArcMap Analysis Tools of the software ArcGIS (ESRI 2014, ArcGIS for Desktop, version 10.3). A distance of 200 m was chosen to minimise spatial overlap of the surroundings and thus to reduce spatial autocorrelation.

Trait data

For each taxonomic group, we selected a set of species traits, which we considered to influence species' responses to urbanisation-related factors. Data of eight plant traits (Table S1) were obtained from the databases TRY (Kattge et al. 2011), LEDA (Kleyer et al. 2008), CLO-PLA (Klimesova and de Bello 2009), BiolFlor (Klotz et al. 2002) and additional information from Landolt et al. (2010) and Müller-Schneider (1986). The following traits were considered to calculate plant functional richness using the *dbFD* function with Cailliez-corrected distance matrices in the package *FD* in R (Laliberté et al. 2014): specific leaf area (SLA), seed dry mass, seed bank longevity index, plant life form, dispersal syndrome, clonal growth organ (CGO), plant tolerance to drought and plant tolerance to human impact (Table S1, S2a).

Data of three traits (body size, dispersal ability and food specialisation) were assembled from literature for orthopteran species (Baur et al. 2006; Reinhardt et al. 2005; Detzel 1998; Bellmann 1985) and lepidopteran species (Schweizerischer Bund für Naturschutz 1987, 1997; Stefanescu et al. 2011; Barbaro and van Halder 2009; Leingärtner et al. 2014; Table 1, S2b, c).

Information on threatened species was obtained from the Red Lists of Switzerland for vascular plants (Bornand et al. 2016), Orthoptera (Monnerat et al. 2007) and diurnal Lepidoptera (Wermeille et al. 2014). Species were considered as threatened if they were classified as critically endangered, endangered, vulnerable or nearly threatened.

Table 1 Species traits of Orthoptera and Lepidoptera

Trait	Type	Description
Orthoptera		
Body size [1]	Categorical	Small (≤ 18 mm); large (> 18 mm)
Dispersal ability [2,3]	Categorical	Low; moderate; high
Food specialisation [1,3,4]	Categorical	Graminivorous; forbivorous; herbivorous; omnivorous
Lepidoptera		
Body size [5]	Categorical	Indicated by wing length: mean forewing length: small (≤ 19 mm); large (> 19 mm)
Dispersal ability [5,6,7,8]	Categorical	Low; moderate; high
Food specialisation [5]	Categorical	Food specialist (monophagy, narrow oligophagy); food generalist (broad oligophagy, polyphagy)

Source: [1] Baur et al. 2006, [2] Reinhardt et al. 2015, [3] Detzel 1998, [4] Bellmann 1985, [5] Schweizerischer Bund für Naturschutz 1987, 1997, [6] Stefanescu et al. 2011, [7] Barbaro and Halder 2009, [8] Leingärtner et al. 2014

Data analyses

Statistical analyses were performed using the software R (R Development Core Team 2013, version 2.15.3) and were carried out separately for the three taxonomic groups and the two habitat types. All analyses were conducted twice, once using the data sets with all sites of the inventory, and once using reduced data sets with only those sites, which contained species of all three taxonomic groups. Both data sets revealed similar results. We, therefore, present only the findings obtained from the entire data sets.

Two approaches were used to examine the relationship between total species richness and habitat size. In the first approach, simple linear regressions were applied with log-transformed data (natural logarithm) of both species number and area (log-log transformed model). In the second approach, log-transformed data of area but untransformed data of species number were used (semi-log transformed model). The first approach allows comparisons of regression lines among taxonomic groups (MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2007), whereas the second approach provided a better fit to the species–area relationship.

Generalized linear models (GLM) with Poisson or quasi-Poisson distributed errors using log-link function were applied to examine potential effects of habitat size and the percentage cover of six landscape elements (sealed area, agricultural area, ruderal area, urban green space, forest, water surface area) within a radius of 200 m on total species richness of the three taxonomic groups and plant functional richness. Preliminary analyses revealed inter-correlations among landscape elements for meadows. Therefore, the percentage cover of agricultural area and forest in all three taxonomic groups as well as the percentage cover of urban green space in Orthoptera and Lepidoptera were excluded from the subsequent GLM analyses. All models were step-wise reduced as recommended by Crawley (2007). Spearman rank correlations were used to examine the relationships between total species richness and those landscape features, which had a significant effect on total species richness in the GLM analyses.

To evaluate whether the landscape features examined influenced the species composition of plants, Orthoptera and Lepidoptera, non-metric multidimensional scaling (NMDS) was used. Species occurring only in one meadow or in one ruderal site were excluded from the subsequent analyses. The ordination was fitted using *metaMDS* function with Euclidean distance and three dimensions in the *vegan* package in R (Oksanen et al. 2013). In a second step, habitat size, perimeter/area ratio and the percentage cover of the six landscape elements were fitted onto the ordinations of the three taxonomic groups using the function *envfit* with 999 permutations in the *vegan* package in R (Oksanen et al. 2013).

Since the response to habitat size may depend on species' traits, simple linear regressions were used to assess the effect of habitat size on the species richness of three traits of Orthoptera and Lepidoptera separately: body size, dispersal ability and food specialisation. In cases of non-normally distributed residuals, GLMs with Poisson or quasi-Poisson distributed errors were applied and species–area relationships of significant traits were tested using Spearman rank correlations. However, no species–area relationships were determined for either forbivorous or herbivorous species of Orthoptera as a consequence of low species number. In Orthoptera, body size was not related to dispersal ability (*Kruskal-Wallis*, $\chi^2 = 2.41$, $df = 2$, $P = 0.30$) and to food specialisation (*Kruskal-Wallis*, $\chi^2 = 7.66$, $df = 3$, $P = 0.054$). Similarly, there was no association between dispersal ability and food specialisation (*Contingency analysis*, $\chi^2 = 5.12$, $df = 6$, $P = 0.53$). In Lepidoptera, however, body size was positively related to dispersal ability (*Kruskal-Wallis*, $\chi^2 = 21.59$, $df = 2$, $P<0.001$). However, food specialisation was neither related to body size (*Kruskal-Wallis*, $\chi^2 = 0.02$, $df = 2$, $P = 0.88$) nor associated with dispersal ability (*Contingency analysis*, $\chi^2 = 1.63$, $df = 2$, $P = 0.44$).

Results

A total of 394 vascular plant species was recorded in 88 habitat sites; 306 species in 60 meadows (77.7%; mean ± se: 26.7 ± 1.3 species per site) and 246 species in 28 ruderal sites (62.4%; 38.2 ± 2.5 species per site). Forty-four of the 394 plant species (11.2%) are considered as threatened in Switzerland (Table S2a).

For Orthoptera, a total of 25 species were recorded in 83 habitat sites; 21 species were found in 58 meadows (84.0%; 6.0 ± 0.4 species per site) and 19 species in 25 ruderal sites (76.0%; 5.4 ± 0.5 species per site). Eleven of the 25 orthopteran species (44.0%) are considered as threatened in Switzerland (Table S2b).

For Lepidoptera, a total of 44 species were recorded in 71 habitat sites; 38 species were found in 52 meadows (86.4%; 7.1 ± 0.5 species per site) and 32 species in 19 ruderal sites (72.7%; 6.3 ± 1.0 species per site). Nine of the 44 lepidopteran species (20.5%) are considered as threatened in Switzerland (Table S2c).

Hypothesis of trophic rank-related species–area relationship

Taxonomic groups were differently affected by the size of the two habitat types (Fig. 2; Table S3, S4). In meadows, positive species–area relationships were obtained for Orthoptera and Lepidoptera using the log-log transformed model (Fig. 2c, e). However, the semi-log transformed model revealed a better fit than the log-log model in the Orthoptera (semi-log: $R^2 = 0.140$; log-log: $R^2 = 0.063$; Fig. S1), whereas both types of model fitted the species–area data of Lepidoptera equally well (semi-log: $R^2 = 0.173$; log-log: $R^2 = 0.174$; Fig. 2e, S1). No species–area relationship could be obtained for vascular plants (Fig. 2a, S1).

In ruderal sites, both types of model showed a positive species–area relationship for vascular plants (Fig. 2b, S1), but the semi-log transformed model fitted the data better (semi-log: $R^2 = 0.393$; log-log:

R^2 = 0.297). For Orthoptera, a positive species–area relationship was obtained in the semi-log transformed model (Fig. S1) but not in the log-log transformed model (Fig. 2d). In Lepidoptera, no species–area relationship could be found (Fig. 2f, S1).

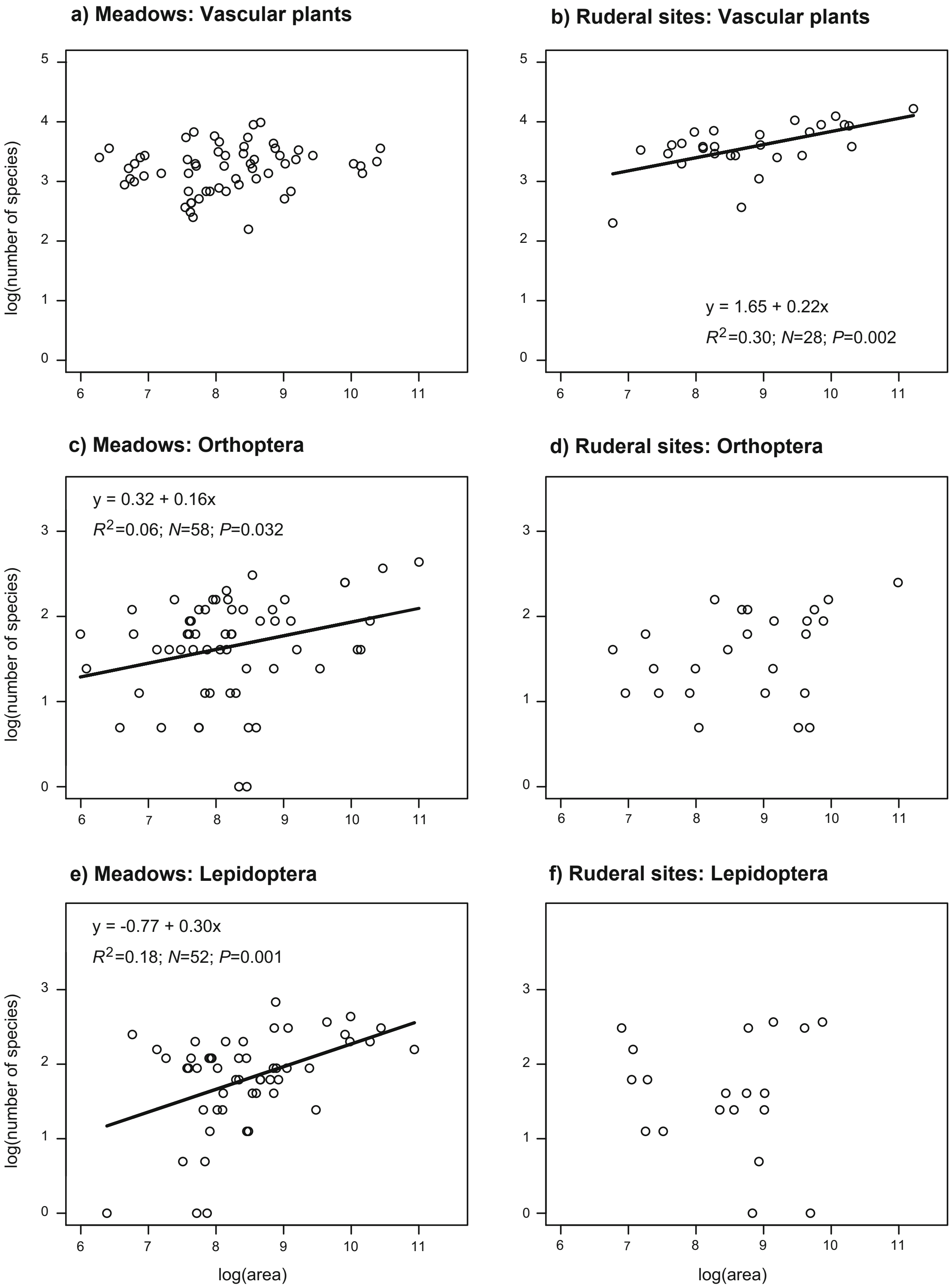


Fig. 2 Species–area relationships (log-log transformed) of vascular plants, Orthoptera and Lepidoptera in meadows and ruderal sites

Surrounding landscape effect hypothesis

Species richness and plant functional richness

Similar effects of habitat size on total species richness of vascular plants, Orthoptera and Lepidoptera were obtained using GLM analyses, which included habitat size and various landscape elements within a radius of 200 m (Table 2). In meadows, the total number of vascular plant species tended to be influenced by the percentage cover of sealed and ruderal area (Table 2a). In addition to the size of meadows, species richness of both Orthoptera and Lepidoptera were negatively affected by the percentage cover of sealed area (Orthoptera: $r_s = -0.72$, $N = 58$, $P<0.001$; Lepidoptera: $r_s = -0.51$, $N = 52$, $P<0.001$, Table 2b, c), but only the number of Lepidoptera species was negatively influenced by the percentage cover of ruderal area ($r_s = -0.33$, $N = 52$, $P<0.018$, Table 2c).

In ruderal sites, orthopteran species richness was negatively correlated with the percentage cover of sealed area ($r_s = -0.47$, $N = 25$, $P<0.019$) and increased with increasing percentage cover of ruderal area in the closer surroundings ($r_s = 0.45$, $N = 25$, $P = 0.024$, Table 2b). Among Lepidoptera, species richness in ruderal sites was significantly influenced by the percentage cover of sealed and agricultural area within a radius of 200 m (Table 2c). Furthermore, the species richness of Lepidoptera increased with increasing percentage cover of ruderal area in the closer surroundings ($r_s = 0.90$, $N = 19$, $P<0.001$, Table 2c). In contrast to species richness of Orthoptera and Lepidoptera, the number of vascular plant species was only affected by the size of ruderal sites but not by any of the six landscape elements examined (Table 2a).

Plant functional richness (FRic) was affected by the size of meadows ($F_{1,58} = 5.48$, $P = 0.023$) but not by any of the six landscape elements examined (Table 2d). However, this finding was mainly due to the influence of a single site. Omitting this site from the analysis, FRic tended to be influenced by the percentage cover of urban green space ($F_{1,57} = 3.76$, $P = 0.057$), but no longer by habitat size (excluded by step-wise reduction of factors). In ruderal sites, FRic increased with increasing habitat size ($F_{1,26} = 4.35$, $P = 0.048$; $r_s = 0.39$, $N = 28$, $P = 0.042$) and decreased with increasing percentage cover of agricultural area ($F_{1,24} = 11.26$, $P = 0.003$; $r_s = -0.43$, $N = 28$, $P = 0.023$). In addition, FRic tended to be influenced by the percentage cover of sealed area ($F_{1,25} = 3.11$, $P = 0.090$; Table 2d).

Interestingly, the percentage cover of urban green space, forest and water surface area did neither affect the species richness of any of the three taxonomic groups nor plant functional richness in meadows and ruderal sites (Table 2).

Species composition

NMDS ordination analyses showed that the species composition of the three taxonomic groups were differently affected by habitat size, perimeter/area ratio and the percentage cover of various landscape characteristics in the closer surroundings of the two habitat types examined (Table S5).

For vascular plants in meadows, species composition was separated along the first NMDS axis by the perimeter/area ratio ($R^2 = 0.16$, $P = 0.010$) and both percentage cover of forest ($R^2 = 0.22$, $P = 0.005$) and water surface area ($R^2 = 0.15$, $P = 0.018$) and along the second NMDS axis by the percentage cover of sealed area within a radius of 200 m ($R^2 = 0.16$, $P = 0.005$; Fig. S2a). In ruderal sites, in contrast, plant species composition was separated by habitat size ($R^2 = 0.47$, $P = 0.002$) and percentage cover of other ruderal areas in the closer surroundings ($R^2 = 0.53$, $P = 0.001$) along the first NMDS axis and was influenced by the perimeter/area ratio ($R^2 = 0.57$, $P = 0.001$) and both percentage cover of urban green space ($R^2 = 0.37$, $P = 0.004$) and water surface area in the closer surroundings along the second NMDS axis ($R^2 = 0.50$, $P = 0.001$; Fig. S2b).

Table 2 Summary of GLM analyses examining the effect of habitat size (log-transformed) and the percentage cover of various landscape elements in the closer surroundings (r = 200 m) on total species richness of (a) vascular plants, (b) Orthoptera and (c) Lepidoptera and (d) plant functional richness in both meadows and ruderal sites

	Meadows			Ruderal sites		
a) Vascular plants	*df*	*F*	*P*	*df*	*F*	*P*
log(habitat size)	–	–	–	1,26	17.95	**<0.001**
Percentage cover of						
sealed area	1,58	2.98	0.090	–	–	–
agricultural area	†	†	†	–	–	–
ruderal area	1,57	2.91	0.094	–	–	–
urban green space	–	–	–	–	–	–
forest	†	†	†	–	–	–
water surface area	–	–	–	–	–	–
b) Orthoptera	*df*	χ^2	*P*	*df*	χ^2	*P*
log(habitat size)	1,56	12.68	**<0.001**	1,23	5.20	**0.023**
Percentage cover of						
sealed area	1,55	36.98	**<0.001**	1,22	5.58	**0.018**
agricultural area	†	†	†	–	–	–
ruderal area	–	–	–	1,21	2.85	0.091
urban green space	†	†	†	–	–	–
forest	†	†	†	–	–	–
water surface area	–	–	–	–	–	–
c) Lepidoptera	*df*	χ^2	*P*	*df*	χ^2	*P*
log(habitat size)	1,50	15.85	**<0.001**	–	–	–
Percentage cover of						
sealed area	1,49	17.18	**<0.001**	1,17	9.54	**0.002**
agricultural area	†	†	†	1,16	8.29	**0.004**
ruderal area	1,48	10.49	**0.001**	1,15	19.36	**<0.001**
urban green space	†	†	†	–	–	–
forest	†	†	†	–	–	–
water surface area	–	–	–	–	–	–
d) Plant functional richness	*df*	*F*	*P*	*df*	*F*	*P*
log(habitat size)	1, 58	5.48	**0.023**	1,26	4.35	**0.048**
Percentage cover of						
sealed area	–	–	–	1,25	3.11	0.090
agricultural area	†	†	†	1,24	11.26	**0.003**
ruderal area	–	–	–	–	–	–
urban green space	–	–	–	–	–	–
forest	†	†	†	–	–	–
water surface area	–	–	–	–	–	–

Significant *P* values (<0.05) are in bold

χ^2-test: GLM with Poisson distributed errors; *F*-test: GLM with quasi-Poisson distributed errors

– factor was excluded from the model by step-wise reduction

† never included in the model

Species composition of both Orthoptera and Lepidoptera was affected along the first NMDS axis by the size and perimeter/area ratio of meadows (Orthoptera: size: $R^2 = 0.30$, $P = 0.001$; ratio: $R^2 = 0.30$, $P = 0.001$; Lepidoptera: size: $R^2 = 0.22$, $P = 0.002$; ratio: $R^2 = 0.20$, $P = 0.003$), and the percentage cover of sealed area (O: $R^2 = 0.53$, $P = 0.001$; L: $R^2 = 0.44$, $P = 0.001$), agricultural area (O: $R^2 = 0.66$, $P = 0.001$; L: $R^2 = 0.27$, $P = 0.001$), urban green space (O: $R^2 = 0.52$, $P = 0.001$; L: $R^2 = 0.14$, $P = 0.038$) and forest (O: $R^2 = 0.13$, $P = 0.027$; L: $R^2 = 0.18$, $P = 0.006$) within a radius of 200 m (Fig. S2c, e).

In ruderal sites, however, species composition of Orthoptera was separated along the first axis by habitat size and perimeter/area ratio (size: $R^2 = 0.42$, $P = 0.005$; ratio: $R^2 = 0.26$, $P = 0.035$) and the percentage cover of agricultural ($R^2 = 0.25$, $P = 0.001$) and ruderal area in the closer surroundings ($R^2 = 0.60$, $P = 0.001$, Fig. S2d), whereas species composition of Lepidoptera was separated along the first NMDS axis by the percentage cover of ruderal area ($R^2 = 0.67$, $P = 0.001$) and along the second NMDS axis by the percentage cover of forest in the closer surroundings ($R^2 = 0.34$, $P = 0.042$, Fig. S2f).

Area-related trait hypothesis

Both small and large orthopteran species showed a positive species–area relationship in meadows (Table 3a, Fig. S3a). The number of species with moderate dispersal abilities was positively affected by meadow size in contrast to species with low and high dispersal abilities (Table 3a, Fig. S3c). Regarding food specialisation, the number of both graminivorous and omnivorous orthopteran species increased with increasing size of meadows (Table 3a, Fig. S3e). In ruderal sites, the species richness of neither small nor large Orthoptera was significantly affected by habitat size (Table 3a, Fig. S3b). In contrast, positive species–area relationships were found for species with moderate and high dispersal abilities but not for species with low dispersal abilities (Table 3a, Fig. S3d). Regarding food specialisation in ruderal sites, the number of omnivorous Orthoptera increased with increasing habitat size, whereas the number of graminivorous species was not affected by habitat size (Table 3a, Fig. S3f).

Among Lepidoptera, the number of species with short wings increased with increasing size of meadows, whereas no species–area relationship was found for species with long wings (Table 3b, Fig. S4a). The species richness of food generalists was positively influenced by meadow size, while the species richness of food specialists only showed a tendency ($r_s = 0.22$, $N = 52$; $P = 0.11$; Table 3b, Fig. S4c). In ruderal sites, however, no species–area relationship was found for either body size or dispersal ability (Table 3b, Fig. S4b, d).

Discussion

The results of our study showed that the responses of species to urbanisation-related factors including habitat size and landscape composition considerably varied depending on the habitat type, taxonomic group and species trait examined.

Hypothesis of trophic rank-related species–area relationship

The theory of island biogeography predicts that larger habitat patches contain more species than smaller habitat patches (MacArthur and Wilson 1967). Indeed, in our study the number of orthopteran and lepidopteran species in meadows and the number of plant and orthopteran species in ruderal sites increased with habitat size, confirming our first hypothesis. Similar findings were reported in Orthoptera in urban grassland fragments (Nufio et al. 2010), in Lepidoptera inhabiting grassland islands in intensively used agricultural areas (Steffan-Dewenter and Tscharntke 2000; Öckinger et al. 2012b) and in plants in urban wasteland sites (Angold et al. 2006; Muratet et al. 2007). In contrast, we did not find any species–area relationships for vascular plants in meadows and for Lepidoptera in ruderal sites.

Table 3 Effect of habitat size (log-transformed) on the number of distinct traits of (a) Orthoptera and (b) Lepidoptera in both meadows and ruderal sites

	Meadows		Ruderal sites	
		P-value		*P*-value
a) Orthoptera	$N = 58$		$N = 25$	
Body size				
small (≤ 18 mm)[a]	$F = 5.31$	**0.025**	$F = 2.50$	0.13
large (>18 mm)[a]	$F = 16.04$	**<0.001**	$F = 3.70$	0.067
Dispersal ability				
low[a,b]	$F = 2.74$	0.10	$\chi^2 = 0.94$	0.33
moderate[a]	$F = 15.92$	**<0.001**	$F = 5.54$	**0.028**
high[b,a]	$\chi^2 = 2.27$	0.13	$F = 7.89$	**0.010**
Food specialisation				
graminivorous[a,c]	$F = 15.61$	**<0.001**	$F = 0.39$	0.54
omnivorous[a]	$F = 6.82$	**0.012**	$F = 4.56$	**0.044**
b) Lepidoptera	$N = 52$		$N = 19$	
Wing length				
short (≤ 19 mm)[a,d]	$F = 15.19$	**<0.001**	$F = 0.02$	0.89
long (> 19 mm)[a,d]	$F = 2.26$	0.14	$F = 0.42$	0.53
Food specialisation				
specialist[a,b]	$\chi^2 = 4.95$	**0.026**	$\chi^2 = 1.39$	0.24
Generalist[a,c]	$F = 8.64$	**0.005**	$F = 0.002$	0.98

Significant *P* values (<0.05) are in bold

N: number of sites

[a] LM [b] GLM with Poisson distributed errors [c] GLM with quasi-Poisson distributed errors [d] log-transformed

For plants, the species–area relationships found in ruderal sites and its absence in meadows may reflect differences in habitat heterogeneity. Ruderal sites are characterized by intense disturbances, which occur at irregular intervals resulting in a high percentage of bare ground. The heterogeneous small-scale distribution of vegetation may reduce competition among different plant species and thus facilitate the colonization by seeds from the closer surroundings and other ruderal sites (Rebele 1994). The meadows examined, on the other hand, are exposed to a moderate level of disturbance (mowing), which occurs at regular intervals, resulting in rather dense and homogeneous cover of vegetation. This may lead to increased competition among plant species and prevent the establishment of seedlings of non-competitive plant species.

Due to their complex life cycle, we expected lepidopteran species to respond more strongly to habitat size than the other two taxonomic groups. While this was the case in meadows, no species–area relationship was recorded in ruderal sites. Findings of studies on Lepidoptera indicate that other factors including habitat heterogeneity (Báldi 2008), habitat quality (Thomas et al. 2001; Öckinger et al. 2006) and landscape fragmentation (Baz and Garcia-Boyero 1995) might be more important for species richness than habitat size per se (Lizée et al. 2012).

Surrounding landscape effect hypothesis

Species richness

Apart from habitat size, the composition of the surrounding landscape may influence the species richness of the three taxonomic groups examined (Steffan-Dewenter 2003; Barbaro and van Halder 2009; Öckinger et al. 2009; Lizée et al. 2012). The percentage cover of sealed area is frequently used as a measure of the level of urbanisation (e.g. McDonnell and Hahs 2008; MacGregor-Fors et al. 2015; Concepción et al. 2016). Hence, we expected species richness of the three taxonomic groups to decrease with sealed area in the surroundings. However, contrary to our second hypothesis and to findings of other urban studies (Albrecht and Haider 2013; Concepción et al. 2016), we did not record any decrease in plant species richness with increasing cover of sealed area in the closer surroundings of either meadows or ruderal sites. There are different explanations for this discrepancy. Godefroid and Koedam (2007) highlighted that some plant groups such as ruderal plants are better adapted to high levels of disturbance due to their short life-cycle and high seed production and thus suffer less from densely sealed areas. Furthermore, dispersal of seeds among habitats may have been more or less restricted in our study depending on the existing type of substrate (asphalt, concrete, cobblestone, sand; Godefroid et al. 2007) and the spatial arrangement of habitat patches (landscape configuration). Consequently, linear habitat strips including road verges and alleys may act as corridors among habitats and thus mitigate isolation effects caused by sealed areas, even if the percentage cover of these strips is relatively low (Tikka et al. 2001; Fischer et al. 2006).

In contrast to plants, we found that the species richness of both Orthoptera and Lepidoptera was negatively affected by the percentage cover of sealed area in the closer surroundings. In both taxonomic groups, the negative effect of nearby-situated sealed areas was more pronounced in meadows than in ruderal sites. This is probably a result of the spatial distribution of the two habitat types. While meadows were more widely distributed across the study area, most ruderal sites were located closer to the city centre and more spatially aggregated (Fig. 1). Thus, ruderal sites were situated in areas with a higher proportion of sealed surfaces and had a low variation among sites compared to meadows. Alternatively, species inhabiting ruderal sites may be better adapted to the living conditions in urban environments and thus tolerate higher amounts of sealed areas than species in meadows.

The cover of sealed area in the surrounding matrix is frequently negatively correlated with the total cover of green area, but not necessarily with different components of green areas (agricultural land, ruderal areas, urban green space, forests) found in cities. These landscape elements can be of different quality for plants, Orthoptera and Lepidoptera and thus may influence their species richness in different ways (second hypothesis). While no effects could be shown for plants and Orthoptera, Lepidoptera species richness in meadows was influenced by the percentage cover of ruderal area and that in ruderal sites by both the percentage cover of agricultural and ruderal area in the closer surroundings, partly confirming our second hypothesis. For some Lepidoptera in ruderal sites, arable land and intensively used meadows in the surrounding matrix may represent unsuitable habitats and thus act as a partial barrier for dispersal (Öckinger et al. 2012b). The findings that Lepidoptera species richness in ruderal sites increased with increasing percentage cover of other ruderal areas in the surroundings can be explained by the foraging behaviour of several species, which also acquire resources from neighbouring ruderal sites. Connectivity among ruderal sites seems to be a better predictor of Lepidoptera species richness than the size of a single habitat patch.

Plant functional richness

Plant functional richness represents the functional niche space that is occupied by the species present and thus can be regarded as the ability of ecosystems to resist environmental fluctuations and the invasion of non-native species (Mason et al. 2005). Plant functional richness is often positively correlated with species richness (Schleuter et al. 2010), as it was the case in our study. This result partly confirms our second hypothesis and may explain the similar effects of habitat size and landscape composition found for plant functional richness and plant species richness. Nevertheless, plant species richness should not be used as a surrogate for plant functional richness, because the negative impact of percentage cover of agricultural area in the closer surroundings of ruderal sites on their plant functional richness could not be predicted based on findings of plant species richness.

Species composition

Different landscape characteristics structured the species composition of plants, Orthoptera and Lepidoptera in meadows and ruderal sites in different ways. Habitat size also affected species composition in groups with positive species–area relationships. Besides habitat size, the perimeter/area ratio influenced species composition of the three taxonomic groups in both habitat types except for Lepidoptera in ruderal sites. This indicates that large and less complex habitat patches not only harboured more but also different species (McKinney and Lockwood; Bommarco et al. 2010; Brückmann et al. 2010; Öckinger et al. 2010) including those that were not able to maintain viable populations in small patches.

In our study, important drivers of species composition in meadows were the percentage cover of both sealed and forest area in the closer surroundings and in ruderal sites the percentage cover of other ruderal areas (Fig. S2). Thus, the effects of various landscape elements on species composition were more consistent within habitat type than within a taxonomic group. This could be explained by the fact that species in a given habitat share common traits and thus respond to the surrounding matrix in a similar way. Our results are supported by the findings of Lizée et al. (2011b), who showed that the habitat and type of land use and to a minor extent the landscape context were directly linked to particular functional traits of Lepidoptera, which in turn resulted in different species assemblages among habitat types. Consequently, effects of the surrounding landscape detected in a particular habitat type cannot be extrapolated to other habitat types.

Area-related trait hypothesis

Based on findings of previous studies (e.g. Steffan-Dewenter and Tscharntke 2000; Öckinger et al. 2010; Nufio et al. 2011), we assumed that certain life-history traits might explain the variability in the species' response to habitat size. In our study, however, the impact of habitat size on the richness of species with particular traits substantially differed between the two habitat types. Thus, our third hypothesis, which tested that large-sized species and species with limited dispersal abilities and high food specialisation were more strongly affected by reduced habitat size, could only be partly confirmed. The most likely reason for these contrasting effects could be differences in species composition between meadows and ruderal sites obtained in preliminary ordination analyses (data not shown). In Orthoptera, however, species with certain traits showed similar responses to habitat size in both meadows and ruderal sites. In line with our third hypothesis, large-sized species of Orthoptera were more strongly affected by the size of meadows and ruderal sites than were small-sized species. Furthermore, in Orthoptera moderate dispersers and omnivorous species also benefitted from increasing habitat size. Surprisingly, however, we did not find any effect of habitat size on the number of species with low dispersal ability, even though this has been repeatedly shown for Orthoptera (Nufio et al. 2011) and other groups of insects (Barbaro and van Halder 2009; Bommarco et al. 2010; Öckinger et al. 2010). This unexpected finding was probably a result of the low number of poor dispersers found in the study sites (Fig. S3). In ruderal sites, species with high dispersal ability also benefitted from increasing habitat size. This indicates that the surrounding matrix represents a more effective barrier for the dispersal of orthopterans among ruderal sites than among meadows.

Contrary to our third hypothesis, we did not detect any species–area relationship for Lepidoptera species with certain traits in ruderal sites. This supports our assumption that species can mitigate potential area effects by acquiring resources from nearby-situated ruderal sites. In our study, many ruderal sites may be too small to provide all necessary resources for the persistence of viable Lepidoptera populations (Dunning et al. 1992; Tscharntke et al. 2002). In meadows, however, short-winged species and both food specialists and generalists benefitted from an increasing area, in line with our third hypothesis. This finding is confirmed by several studies examining the effects of habitat size on life-history traits of Lepidoptera (e.g. Steffan-Dewenter and Tscharntke 2000; Öckinger et al. 2010). However, the more pronounced response of food generalists to habitat size contradicts other studies in Lepidoptera (Steffan-Dewenter and Tscharntke 2000; Öckinger et al. 2010). This may be due to the low number of food specialists found in the meadows examined.

Conclusions

By the year 2050, 66 per cent of the world's population is predicted to live in cities (United Nations 2014) with the consequence that the pressure on the remaining urban green sites will increase. The identification of the drivers of urban biodiversity is therefore of increasing importance. Our study demonstrated that vascular plants, Orthoptera and Lepidoptera were differently affected by habitat size and landscape composition in meadows and ruderal sites, which could be partly explained by differences in species composition and species traits. Both meadows and ruderal sites exhibited a considerable diversity in flora and fauna including several endangered species (Reisner et al. 2013; Table S2). Conservation measures in urban areas mainly focus on semi-natural habitats such as meadows and forests, while ruderal sites are frequently neglected (Muratet et al. 2007; Knapp et al. 2008). The fact that species in ruderal sites responded differently to urbanisation-related factors than species in meadows highlights the importance to develop habitat-specific conservation plans. We recommend that urban planners develop more flexible management strategies to satisfy the different requirements of various taxonomic groups. To sustain a high level of urban biodiversity, these plans should also consider enhancing the quality of other green sites surrounding the target habitat.

Acknowledgements

We thank Y. Reisner and C. Farrèr for answering questions regarding the inventory and A. Baur, B. Braschler and two anonymous reviewers for comments on the manuscript. Financial support was received from the Stadtgärtnerei Basel.

References

Albrecht H, Haider S (2013) Species diversity and life history traits in calcareous grasslands vary along an urbanization gradient. Biodivers Conserv 22:2243–2267

Angold PG, Sadler JP, Hill MO, Pullin A, Rushton S, Austin K, Small E, Wood B, Wadsworth R, Sanderson R, Thompson K (2006) Biodiversity in urban habitat patches. Sci Total Environ 360:196–204

Báldi A (2008) Habitat heterogeneity overrides the species–area relationship. J Biogeogr 35:675–681

Barbaro L, van Halder I (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32:321–333

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85:2671–2676

Baur B, Baur H, Roesti C, Roesti D (2006) Die Heuschrecken der Schweiz, 1st edn. Haupt, Bern

Baz A, Garcia-Boyero A (1995) The effects of forest fragmentation on butterfly communities in central Spain. J Biogeogr 22:129–140

Bellmann H (1985) Heuschrecken: beobachten – bestimmen, 1st edn. Neumann-Neudamm, Melsungen

Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. Biol Conserv 80:113–125

Bommarco R, Biesmeijer JC, Meyer B, Potts SG, Pöyry J, Roberts SPM, Steffan-Dewenter I, Öckinger E (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proc Roy Soc B 277:2075–2082

Bornand C, Gygax A, Juillerat P, Jutzi M, Möhl A, Rometsch S, Sager L, Santiago H, Eggenberg S (2016) Rote Liste Gefässpflanzen. Gefährdete Arten der Schweiz. Bundesamt für Umwelt, Bern und Info Flora, Genf. Umwelt-Vollzug Nr. 1621

Brückmann SV, Krauss J, Steffan-Dewenter I (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. J Appl Ecol 47:799–809

Concepción ED, Obrist MK, Moretti M, Altermatt F, Baur B, Nobis MP (2016) Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosyst 19:225–242

Crawley MJ (2007) The R Book. Wiley, Chichester

Detzel P (1998) Die Heuschrecken Baden-Württembergs. Ulmer, Stuttgart

Deutschewitz K, Lausch A, Kühn I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Global Ecol Biogeogr 12:299–311

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

ESRI (2014) ArcGIS Desktop: Release 10.3. Environmental Systems Research Institute, Redlands CA. URL: http://www.esri.com/software/arcgis/arcgis-for-desktop

Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front Ecol Environ 4:80–86

Fischer LK, von der Lippe M, Kowarik I (2013) Urban land use types contribute to grassland conservation: the example of Berlin. Urban For Urban Green 12:263–272

GEO BL (2014) https://www.geo.bl.ch. Accessed 27 Oct 2014

Geoportal Baden-Württemberg (2014) https://www.lgl-bw.de. Accessed 29 Oct 2014

Geoportal Kanton Basel-Stadt (2014) http://shop.geo.bs.ch/geoshop_app/geoshop. Accessed 8 July 2014

Germann C, Sattler T, Obrist MK, Moretti M (2008) Xero-thermophilous and grassland ubiquist species dominate the weevil fauna of Swiss cities (Coleoptera, Curculionoidea). Mitt Schweiz Entomol Ges 81:141–154

Godefroid S, Koedam N (2007) Urban plant species patterns are highly driven by density and function of built-up areas. Landscape Ecol 22:1227–1239

Godefroid S, Monbaliu D, Koedam N (2007) The role of soil and microclimatic variables in the distribution patterns of urban wasteland flora in Brussels, Belgium. Landscape Urban Plan 80:45–55

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu JG, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760

Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, van Bodegom PM, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly DD, Anand M, Atkin O, Bahn M, Baker TR, Baldocchi D, Bekker R, Blanco CC, Blonder B, Bond WJ, Bradstock R, Bunker DE, Casanoves F, Cavender-Bares J, Chambers JQ, Chapin FS, Chave J, Coomes D, Cornwell WK, Craine JM, Dobrin BH, Duarte L, Durka W, Elser J, Esser G, Estiarte M, Fagan WF, Fang J, Fernández-Méndez F, Fidelis A, Finegan B, Flores O, Ford H, Frank D, Freschet GT, Fyllas NM, Gallagher RV, Green WA, Gutierrez AG, Hickler T, Higgins SI, Hodgson JG, Jalili A, Jansen S, Joly CA, Kerkhoff AJ, Kirkup D, Kitajima K, Kleyer M, Klotz S, Knops JMH, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee TD, Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, Llusià J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, Müller SC, Nadrowski K, Naeem S, Niinemets U, Nöllert S, Nüske A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, Ordoñez J, Overbeck G, Ozinga WA, Patiño S, Paula S, Pausas JG, Peñuelas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negre B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana JF, Swaine E, Swenson N, Thompson

K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY – a global database of plant traits. Glob Change Biol 17:2905–2935. www.try-db.org. Accessed 15 Sept 2015

Kattwinkel M, Strauss B, Biedermann R, Kleyer M (2009) Modelling multi-species response to landscape dynamics: mosaic cycles support urban biodiversity. Landscape Ecol 24:929–941

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel AK, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274. http://www.uni-oldenburg.de/en/landeco/research/projects/LEDA. Accessed 15 Sept 2015

Klimesova J, de Bello F (2009) CLO-PLA: the database of clonal and bud bank traits of Central European flora. J Veg Sci 20:511–516. http://clopla.butbn.cas.cz. Accessed 15 Sept 2015

Klotz S, Kühn I, Durka W (2002) BIOLFLOR - Eine Datenbank mit biologisch-Ökologischen Merkmalen der Gefässpflanzen in Deutschland. - Schriftenreihe für Vegetationskunde 38, Bundesamt für Naturschutz. Bonn. http://www2.ufz.de/biolflor. Accessed 1 Oct 2015

Knapp S, Kühn I, Mosbrugger V, Klotz S (2008) Do protected areas in urban and rural landscapes differ in species diversity? Biodivers Conserv 17:1595–1612

Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. Environ Pollut 159:1974–1983

Kühn I, Brandl R, Klotz S (2004) The flora of German cities is naturally species rich. Evol Ecol Res 6:749–764

Laliberté E, Legendre P, Shipley B (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://cran.r-project.org/web/packages/FD/. Accessed 10 Feb 2016

Landolt E, Bäumler B, Erhardt A, Hegg O, Kötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schweingruper FH, Theurillat JP, Urmi E, Vust M, Wohlgemuth T (2010) Flora Indicativa, 2nd edn. Haupt, Bern

Leingärtner A, Krauss J, Steffan-Dewenter I (2014) Species richness and trait composition of butterfly assemblages change along an altitudinal gradient. Oecologia 175:613–623

Lizée MH, Bonardo R, Mauffrey JF, Bertaudière-Montes V, Tatoni T, Deschamps-Cottin M (2011a) Relative importance of habitat and landscape scales on butterfly communities of urbanizing areas. C R Biol 334:74–84

Lizée MH, Mauffrey JF, Tatoni T, Deschamps-Cottin M (2011b) Monitoring urban environments on the basis of biological traits. Ecol Indic 11:353–361

Lizée MH, Manel S, Mauffrey JF, Tatoni T, Deschamps-Cottin M (2012) Matrix configuration and patch isolation influences override the species–area relationship for urban butterfly communities. Landscape Ecol 27:159–169

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton NJ

MacGregor-Fors I, Avendaño-Reyes S, Bandala VM, Chacón-Zapata S, Díaz-Toribio MH, González-García F, Lorea-Hernández F, Martínez-Gómez J, de Oca EM, Montoya L, Pineda E, Ramírez-Restrepo L, Rivera-García E, Utrera-Barrillas E, Escobar F (2015) Multi-taxonomic diversity patterns in a neotropical green city: a rapid biological assessment. Urban Ecosyst 18:633–647

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecol 23:1143–1155

McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience 52:883–890

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

MeteoSwiss (2016) Climate normals Basel/Binningen, reference period 1981–2010. Federal office of meteorology and climatology MeteoSwiss. http://www.meteoswiss.admin.ch. Accessed 26 May 2016

Monnerat C, Thorens P, Walter T, Gonsetz Y (2007) Rote Liste der Heuschrecken der Schweiz. Bundesamt für Umwelt, Bern, und Schweizer Zentrum für die Kartographie der Fauna, Neuenburg. Umwelt-Vollzug 0719

Müller N, Ignatieva M, Nilon CH, Werner P, Zipperer WC (2013) Patterns and trends in urban biodiversity and landscape design. In: Elmqvist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (eds) Urbanization, biodiversity and ecosystem services: challenges and opportunities. Springer, Heidelberg, pp 123–174

Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens, 85. Heft. Veröffentl Geobot Inst ETH, Stiftung Rübel, Zürich

Muratet A, Machon N, Jiguet F, Moret J, Porcher E (2007) The role of urban structures in the distribution of wasteland flora in the greater Paris area, France. Ecosystems 10:661–671

Niemelä J (1999) Ecology and urban planning. Biodivers Conserv 8:119–131

Nufio CR, McClenahan JL, Bowers MD (2011) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. J Insect Conserv 15:409–419

Öckinger E, Hammarstedt O, Nilsson SG, Smith HG (2006) The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. Biol Conserv 128:564–573

Öckinger E, Dannestam A, Smith HG (2009) The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landscape Urban Plan 93:31–37

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol Lett 13:969–979

Öckinger E, Bergman KO, Franzén M, Kadlec T, Krauss J, Kuussaari M, Pöyry J, Smith HG, Steffan-Dewenter I, Bommarco R (2012a) The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. Landscape Ecol 27:121–131

Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012b) Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography 35:259–267

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos R, Stevens MHH, Wagner H (2013) Vegan: community ecology package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan. Accessed 12 Oct 2015

Pyšek P (1998) Alien and native species in Central European urban floras: a quantitative comparison. J Biogeogr 25:155–163

R Development Core Team (2013) R: a language and environment for statistical computing, version 2.15.3. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Rebele F (1994) Urban ecology and special features of urban ecosystems. Global Ecol Biogeogr 4:173–187

Reinhardt K, Köhler G, Maas S, Detzel P (2005) Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28:593–602

Reisner Y, Plattner M, Berney C, Birrer S, Farrèr C, Frei M, Küry D, Ramseier P, Steck C, Zemp M (2013) Unbekannte Schätze vor der Haustür – Ergebnisse des Naturinventars im Kanton Basel-Stadt. Bau- und Verkehrsdepartement des Kanton Basel-Stadt, Stadtgärtnerei, Basel

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99

Sattler T, Duelli P, Obrist MK, Arlettaz R, Moretti M (2010) Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecol 25:941–954

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecol Monogr 80:469–484

Schweizerischer Bund für Naturschutz (1987) Tagfalter und ihre Lebensräume, Band 1, FO-Publishing, Zürich

Schweizerischer Bund für Naturschutz (1997) Schmetterlinge und ihre Lebensräume, Band 3, FO-Publishing, Zürich

Soga M, Yamaura Y, Koike S, Gaston KJ (2014) Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? J Appl Ecol 51:1378–1386

Statistisches Amt Kanton Basel-Stadt (2015) Tabellen: Bevölkerung; Bodennutzung; Pendler. http://www.statistik.bs.ch/zahlen/tabellen.html. Accessed 26 May 2016

Stefanescu C, Carnicer J, Peñuelas J (2011) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. Ecography 34:353–363

Steffan-Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv Biol 17:1036–1044

Steffan-Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3:449–456

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc Roy Soc B 268:1791–1796

Tikka PM, Högmander H, Koski PS (2001) Road and railway verges serve as dispersal corridors for grassland plants. Landscape Ecol 16:659–666

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: A mini review. Ecol Res 17:229–239

(UN) United Nations (2014) World urbanization prospects, the 2014 revision. http://esa.un.og/unpd/wup. Accessed 26 May 2016

Van Noordwijk CGE, Verberk WCEP, Turin H, Heijerman T, Alders K, Dekoninck W, Hannig K, Regan E, McCormack S, Brown MJF, Remke E, Siepel H, Berg MP, Bonte D (2015) Species–area relationships are modulated by trophic rank, habitat affinity, and dispersal ability. Ecology 96:518–531

Wania A, Kühn I, Klotz S (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. Landscape Urban Plan 75:97–110

Wermeille E, Chittaro Y, Gonseth Y (2014) Rote Liste Tagfalter und Widderchen. Gefährdete Arten der Schweiz, Stand 2012. Bundesamt für Umwelt, Bern, und Schweizer Zentrum für die Kartografie der Fauna, Neuenburg. Umwelt-Vollzug Nr. 1403

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: Ecology, evolution and conservation, 2nd edn. Oxford University Press, Oxford

Wittig R (2002) Siedlungsvegetation. Ulmer, Stuttgart

Supplementary material Chapter I

Table S1	Functional traits of vascular plants
Table S2	Species list of vascular plants, Orthoptera and Lepidoptera and the traits used for the corresponding taxonomic groups
Table S3/S4	Two tables showing the summary of linear regressions of the log-log and semi-log transformed model
Table S5	Summary of the results of the *envfit*-function (species composition)

Figure S1	Species–area relationships (semi-log transformed model) of vascular plants, Orthoptera and Lepidoptera
Figure S2	NMDS ordination diagrams for plants, Orthoptera and Lepidoptera
Figure S3	Species–area relationships of traits of orthopteran species examined
Figure S4	Species–area relationships of traits of lepidopteran species examined

Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape

Ramona Laila Melliger, Hans-Peter Rusterholz, Bruno Baur

Table S1 Functional traits of vascular plants

Trait	Type	Description
Specific leaf area (SLA) [1]	Continuous	Mean of SLA-values
Seed dry mass (mg) [1]	Continuous	Mean of seed mass-values
Seed bank longevity index [2,3]	Continuous	From 0 (strictly transient) to 1 (strictly persistent)
Plant life form [4]	Categorical	Phanerophyte; nanophanerophyte; chamaephyte; hemikryptophyte; geophyte; therophyte; hydrophyte
Dispersal syndrome [4,5]	Categorical	Autochory; zoochory; anemochory; hydrochory; hemerochory
Clonal growth organ (CGO) [6]	Categorical	Runner; rhizome; bulb & tuber; root; no clonal growth organ
Plant tolerance to drought [1]	Categorical	Low; medium; high
Plant tolerance to human impact [4,7]	Categorical	Urbanophobic; moderately urbanophobic; urbanoneutral; moderately urbanophilic; urbanophilic

Source: [1] TRY, [2] LEDA, [3] Bekker et al. 1998, [4] Landolt et al. 2010, [5] Müller-Schneider (1986), [6] CLO-PLA, [7] BiolFlor

References

[1] Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Bönisch G et al. (2011) TRY – a global database of plant traits. Glob Change Biol 17:2905–2935. www.try-db.org. Accessed 15 September 2015

[2] Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M et al. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274. http://www.uni-oldenburg.de/en/landeco/research/projects/LEDA. Accessed 15 September 2015

[3] Bekker RM, Bakker JP, Grandin U, Kalamees R, Milberg P, Poschlod P, Thompson K, Willems JH (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Funct Ecol 12:834–842

[4] Landolt E, Bäumler B, Erhardt A, Hegg O, Kötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schweingruper FH, Theurillat JP, Urmi E, Vust M, Wohlgemuth T (2010) Flora Indicativa, 2nd edn. Haupt, Bern

[5] Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens, 85. Heft. Veröffentl Geobot Inst ETH, Stiftung Rübel, Zürich

[6] Klimesova J, de Bello F (2009) CLO-PLA: the database of clonal and bud bank traits of Central European flora. J Veg Sci 20:511–516. http://clopla.butbn.cas.cz. Accessed 15 September 2015

[7] Klotz S, Kühn I, Durka W (2002) BIOLFLOR - Eine Datenbank mit Biologisch-Ökologischen Merkmalen zur Flora von Deutschland. LandWirtschaftsverlag, Bonn. http://www2.ufz.de/biolflor. Accessed 1 October 2015

Table S2 Species list of (a) vascular plants, (b) Orthoptera and (c) Lepidoptera. The occurrence in the two habitat types (m = meadows; r = ruderal sites) and the traits used for analyses are given. (Red List: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered; Tolerance to human impact: 1 = urbanophobic, 2 = moderately urbanophobic, 3 = urbanoneutral, 4 = moderately urbanophilic, 5 = urbanophilic)

a) Vascular plants

Species	**Habitat type**	**Red List**	**SLA**	**Seed mass**	**Longevity index**	**Plant life form**	**Dispersal syndrom**	**CGO**	**Tolerance to drought**	**Tolerance to human impact**
Acer campestre	m	LC	17.72	78.89	0.00	phanerophyte	anemochory	root	medium	2
Acer platanoides	m	LC	22.00	127.33	0.00	phanerophyte	anemochory	root	medium	3
Acer pseudoplatanus	m	LC	16.94	92.46	0.00	phanerophyte	anemochory	root	medium	3
Achillea millefolium	m, r	LC	15.32	0.18	0.10	chamaephyte	anemochory	rhizome	medium	3
Acinos arvensis	m, r	LC	18.57	0.38	0.50	chamaephyte	zoochory	rhizome	–	2
Agrimonia eupatoria	m	LC	18.72	15.24	0.03	hemicryptophyte	zoochory	rhizome	–	2
Agrostemma githago	r	EN	16.30	14.29	0.27	therophyte	zoochory	none	–	2
Agrostis capillaris	m	LC	32.20	0.11	0.52	hemicryptophyte	anemochory	rhizome	low	3
Agrostis stolonifera	r	LC	28.99	0.05	0.38	hemicryptophyte	anemochory	runner	low	3
Ailanthus altissima	r	–	14.30	29.36	1.00	phanerophyte	anemochory	root	medium	5
Alchemilla xanthochlora aggr.	m	LC	19.94	0.41	–	hemicryptophyte	anemochory	rhizome	–	2
Alliaria petiolata	m	LC	46.59	2.50	0.29	hemicryptophyte	anemochory	root	–	2
Allium oleraceum	m, r	LC	11.80	11.34	0.00	geophyte	hemerochory	bulb&tuber	–	2
Allium scorodoprasum	m	NT	4.83	11.87	0.00	geophyte	anemochory	bulb&tuber	–	2
Allium vineale	m, r	LC	18.70	12.39	0.08	geophyte	anemochory	bulb&tuber	–	1
Alnus glutinosa	r	LC	19.47	2.02	0.45	phanerophyte	anemochory	root	medium	2
Alnus incana	r	LC	20.57	1.00	0.50	phanerophyte	anemochory	rhizome	low	2
Alopecurus aequalis	m	VU	24.81	0.23	0.71	hemicryptophyte	anemochory	runner	low	2
Alopecurus pratensis	m	LC	24.23	0.77	0.09	hemicryptophyte	anemochory	rhizome	low	2
Amaranthus albus	r	–	–	0.32	1.00	therophyte	zoochory	none	–	5
Anacamptis pyramidalis	m	NT	46.85	–	–	geophyte	anemochory	root	–	1
Anemone nemorosa	m	LC	30.83	2.55	0.03	geophyte	zoochory	rhizome	–	2
Angelica sylvestris	r	LC	24.41	1.83	0.13	hemicryptophyte	anemochory	rhizome	–	1
Anthemis tinctoria	m, r	LC	18.35	0.53	0.50	chamaephyte	zoochory	none	–	2

Anthoxanthum odoratum	m	LC	28.00	0.54	0.28	hemicryptophyte	anemochory	rhizome	–	2
Anthyllis vulneraria s.l.	m, r	LC	15.51	3.04	0.11	hemicryptophyte	anemochory	none	–	1
Aphanes arvensis	m	LC	23.86	0.23	0.83	therophyte	anemochory	none	–	2
Aquilegia vulgaris	m, r	LC	33.55	1.57	0.00	hemicryptophyte	anemochory	root	–	2
Arabidopsis thaliana	m, r	LC	32.77	0.02	0.67	therophyte	anemochory	none	–	3
Arabis hirsuta	m, r	LC	30.99	0.12	0.74	hemicryptophyte	anemochory	rhizome	–	1
Arabis turrita	r	LC	25.61	0.54	–	hemicryptophyte	anemochory	root	–	1
Arctium lappa	m, r	LC	24.67	11.84	0.72	hemicryptophyte	zoochory	none	–	4
Arctium minus	m, r	LC	23.91	10.07	0.67	hemicryptophyte	zoochory	none	–	4
Arenaria leptoclados	m, r	LC	–	0.04	–	therophyte	anemochory	none	–	2
Arenaria serpyllifolia aggr.	m, r	LC	21.24	0.07	0.65	therophyte	anemochory	none	–	2
Artemisia vulgaris	m, r	LC	19.52	0.15	0.35	hemicryptophyte	anemochory	root	–	4
Asparagus officinalis	m, r	LC	11.03	20.13	0.00	geophyte	zoochory	rhizome	–	2
Asplenium adiantum-nigrum	r	LC	–	–	–	hemicryptophyte	anemochory	rhizome	–	1
Asplenium ruta-muraria	r	LC	14.66	–	–	hemicryptophyte	anemochory	rhizome	–	4
Asplenium trichomanes	r	LC	19.44	–	–	hemicryptophyte	anemochory	rhizome	–	1
Astragalus glycyphyllos	m, r	LC	26.24	5.09	0.22	hemicryptophyte	anemochory	none	–	2
Ballota nigra ssp. *foetida*	m	NT	21.25	0.95	0.63	geophyte	zoochory	none	–	4
Barbarea vulgaris	m	LC	24.64	0.64	0.31	hemicryptophyte	anemochory	rhizome	–	3
Berteroa incana	m, r	–	19.46	0.57	0.25	hemicryptophyte	anemochory	none	–	3
Betula pendula	m	LC	11.84	0.27	0.75	phanerophyte	anemochory	rhizome	low	3
Brachypodium pinnatum	m	LC	24.71	2.95	0.05	hemicryptophyte	anemochory	rhizome	–	2
Briza media	m	LC	23.37	0.37	0.02	hemicryptophyte	anemochory	rhizome	–	2
Bromus erectus	m, r	LC	16.22	3.82	0.10	hemicryptophyte	anemochory	rhizome	–	2
Bromus sterilis	r	LC	33.52	6.07	0.00	therophyte	anemochory	rhizome	–	3
Bromus tectorum	m, r	LC	29.34	2.85	0.25	therophyte	anemochory	rhizome	–	3
Bryonia dioica	m	LC	–	12.97	–	hemicryptophyte	zoochory	root	–	3
Buddleja davidii	r	–	18.77	0.26	0.25	nanophanerophyte	anemochory	–	high	5
Bunias orientalis	m, r	–	23.63	25.40	0.00	hemicryptophyte	zoochory	root	–	3
Buxus sempervirens	m	NT	7.88	24.70	0.00	nanophanerophyte	zoochory	–	high	2
Calamagrostis epigejos	m, r	LC	22.04	0.07	0.14	geophyte	anemochory	rhizome	–	3
Calamintha menthifolia	r	LC	–	–	–	geophyte	zoochory	–	–	1

Campanula glomerata	m	LC	21.24	0.14	0.50	hemicryptophyte	anemochory	rhizome	–	1
Campanula patula	m	LC	46.26	0.02	0.54	hemicryptophyte	anemochory	rhizome	–	2
Campanula persicifolia	m	LC	16.77	0.08	0.39	hemicryptophyte	anemochory	rhizome	–	2
Campanula rapunculoides	m	LC	52.66	0.15	0.13	geophyte	anemochory	rhizome	–	3
Campanula rapunculus	m, r	LC	39.93	0.03	0.00	hemicryptophyte	anemochory	none	–	1
Campanula rotundifolia	m, r	LC	26.14	0.06	0.38	hemicryptophyte	anemochory	rhizome	–	2
Carduus crispus	m	LC	23.60	1.68	0.38	hemicryptophyte	anemochory	none	–	2
Carex acutiformis	m, r	LC	15.70	0.88	0.10	geophyte	anemochory	rhizome	–	2
Carex caryophyllea	m	LC	21.36	1.03	0.22	hemicryptophyte	zoochory	rhizome	–	1
Carex flacca	m	LC	16.21	0.84	0.34	geophyte	anemochory	rhizome	–	1
Carex hirta	m, r	LC	18.27	2.38	0.19	geophyte	anemochory	rhizome	–	3
Carex muricata aggr.	m	LC	17.07	1.77	0.67	hemicryptophyte	anemochory	rhizome	–	2
Carex ornithopoda	m	LC	30.60	0.84	0.00	hemicryptophyte	zoochory	rhizome	–	1
Carex pendula	r	LC	13.30	0.68	0.71	hemicryptophyte	anemochory	rhizome	–	1
Carex sylvatica	m	LC	23.48	1.51	0.71	hemicryptophyte	zoochory	rhizome	–	1
Carlina vulgaris	r	LC	22.17	1.43	0.50	hemicryptophyte	anemochory	root	–	2
Carpinus betulus	m	LC	25.32	44.81	0.00	phanerophyte	anemochory	root	medium	2
Catapodium rigidum	r	LC	17.45	0.23	–	therophyte	anemochory	rhizome	–	2
Centaurea cyanus	m, r	NT	22.00	5.28	0.61	therophyte	anemochory	none	–	2
Centaurea jacea s.l.	m, r	LC	20.04	1.55	0.10	hemicryptophyte	anemochory	rhizome	–	2
Centaurea scabiosa	m, r	LC	16.46	6.71	0.10	hemicryptophyte	zoochory	root	–	2
Centaurea stoebe	m, r	VU	21.34	–	–	hemicryptophyte	anemochory	rhizome	–	2
Centaurium erythraea	m	LC	25.13	0.01	0.80	therophyte	anemochory	none	–	2
Cephalanthera damasonium	m	LC	31.00	0.01	–	geophyte	anemochory	rhizome	–	1
Cerastium arvense	m	LC	20.47	0.19	0.36	chamaephyte	anemochory	none	–	3
Cerastium brachypetalum	m, r	LC	21.92	0.06	0.40	therophyte	anemochory	none	–	2
Cerastium pumilum aggr.	r	NT	28.69	0.05	0.22	therophyte	anemochory	none	–	1
Cerastium semidecandrum	m, r	LC	17.96	0.04	0.22	therophyte	anemochory	none	–	2
Chaenorrhinum minus	r	LC	–	–	–	therophyte	anemochory	–	–	5
Chaerophyllum aureum	m, r	LC	20.14	8.05	0.50	hemicryptophyte	anemochory	rhizome	–	2
Chaerophyllum temulum	m	LC	27.57	2.41	0.58	therophyte	anemochory	none	–	3
Chelidonium majus	m	LC	38.03	0.74	0.62	hemicryptophyte	zoochory	rhizome	–	4

Chenopodium strictum	r	–	–	0.33	–	therophyte	zoochory	none	–	5
Chondrilla juncea	r	NT	8.89	0.44	0.00	hemicryptophyte	anemochory	none	–	2
Cichorium intybus	m, r	LC	24.08	2.27	0.10	hemicryptophyte	anemochory	root	medium	3
Cirsium acaule	m	LC	12.65	3.86	0.00	hemicryptophyte	anemochory	rhizome	–	1
Cirsium vulgare	m, r	LC	15.34	2.58	0.21	hemicryptophyte	anemochory	none	–	3
Clematis vitalba	m, r	LC	27.40	2.42	0.20	phanerophyte	anemochory	–	–	3
Clinopodium vulgare	m, r	LC	24.98	0.40	0.50	geophyte	anemochory	rhizome	–	1
Colchicum autumnale	m	LC	21.63	5.89	0.00	geophyte	zoochory	bulb&tuber	–	1
Convallaria majalis	m	LC	29.50	37.28	0.14	geophyte	zoochory	rhizome	low	2
Cornus sanguinea	m	LC	22.22	63.74	0.03	nanophanerophyte	zoochory	root	medium	2
Corylus avellana	m	LC	22.35	1012.63	0.00	nanophanerophyte	zoochory	root	medium	2
Crataegus laevigata	m	LC	20.34	164.53	0.07	nanophanerophyte	zoochory	–	medium	2
Crataegus monogyna	m, r	LC	13.06	118.53	0.03	nanophanerophyte	zoochory	–	high	2
Crepis biennis	m	LC	30.85	1.17	0.00	hemicryptophyte	anemochory	none	–	3
Crepis foetida	m, r	LC	20.79	0.55	1.00	therophyte	anemochory	none	–	2
Crepis pulchra	m, r	–	–	0.41	0.25	therophyte	anemochory	none	–	3
Crepis setosa	m, r	–	30.77	–	–	therophyte	anemochory	none	–	4
Crepis vesicaria ssp. *taraxacifolia*	r	LC	20.86	0.35	0.00	hemicryptophyte	anemochory	–	–	3
Cruciata laevipes	m	LC	27.19	3.80	0.00	geophyte	zoochory	rhizome	–	2
Cymbalaria muralis	m, r	LC	24.87	0.16	0.00	chamaephyte	autochory	none	–	4
Cynodon dactylon	r	LC	28.39	0.18	0.50	geophyte	anemochory	rhizome	medium	4
Dactylis polygama	m	NT	39.50	–	–	hemicryptophyte	anemochory	rhizome	–	1
Dactylorhiza fuchsii	m	LC	23.20	–	0.00	geophyte	anemochory	root	–	1
Daucus carota	m, r	LC	18.83	1.11	0.32	hemicryptophyte	zoochory	root	–	3
Deschampsia cespitosa	m	LC	16.93	0.24	0.27	hemicryptophyte	anemochory	rhizome	–	2
Dianthus armeria	m	LC	15.66	0.57	–	hemicryptophyte	anemochory	–	–	1
Dianthus carthusianorum s.l.	m, r	LC	17.71	1.26	0.00	hemicryptophyte	anemochory	runner	–	2
Diplotaxis tenuifolia	m, r	LC	22.45	0.29	0.00	hemicryptophyte	anemochory	none	–	4
Dipsacus fullonum	m, r	LC	19.55	2.25	0.10	hemicryptophyte	zoochory	–	–	3
Draba muralis	m, r	NT	26.10	0.06	–	therophyte	anemochory	none	–	4
Dryopteris filix-mas	m	LC	36.67	–	–	hemicryptophyte	anemochory	rhizome	–	2
Echium vulgare	m, r	LC	15.94	3.03	0.29	hemicryptophyte	anemochory	none	–	3

Eleocharis palustris aggr.	m	NT	13.72	0.85	0.22	geophyte	zoochory	rhizome	low	2
Elymus repens	m, r	LC	26.24	3.05	0.07	geophyte	anemochory	–	low	3
Epilobium ciliatum	r	–	41.32	0.08	0.98	hemicryptophyte	anemochory	runner	–	3
Epilobium dodonaei	r	NT	11.60	0.25	–	chamaephyte	anemochory	rhizome	–	2
Epilobium hirsutum	r	LC	27.87	0.12	0.64	hemicryptophyte	anemochory	rhizome	–	2
Equisetum arvense	m	LC	13.52	–	–	geophyte	anemochory	rhizome	low	3
Eragrostis pilosa	r	LC	42.12	0.05	0.00	therophyte	anemochory	rhizome	–	5
Eranthis hyemalis	m	LC	–	4.20	–	geophyte	hemerochory	bulb&tuber	–	2
Erigeron acer	m, r	LC	18.74	0.10	0.00	hemicryptophyte	anemochory	–	–	3
Erigeron annuus s.l.	m, r	–	25.50	0.04	0.41	hemicryptophyte	anemochory	none	–	3
Eriophorum angustifolium	m	LC	10.64	0.60	0.10	geophyte	anemochory	rhizome	low	1
Erodium cicutarium	m, r	LC	29.91	1.86	0.15	therophyte	zoochory	none	–	3
Erophila praecox	m, r	LC	–	–	–	therophyte	anemochory	–	–	3
Erophila verna aggr.	m, r	LC	39.75	0.52	0.31	therophyte	anemochory	none	–	2
Euonymus europaea	m	LC	–	31.34	–	nanophanerophyte	zoochory	–	–	2
Eupatorium cannabinum	r	LC	26.48	0.43	0.46	hemicryptophyte	anemochory	rhizome	–	2
Euphorbia cyparissias	m	LC	23.40	2.12	0.21	hemicryptophyte	autochory	rhizome	–	2
Euphorbia dulcis	m	LC	44.62	2.12	–	geophyte	autochory	rhizome	–	1
Euphorbia helioscopia	r	LC	35.52	2.37	0.63	therophyte	autochory	root	–	3
Euphorbia stricta	r	LC	–	0.61	–	therophyte	autochory	–	–	2
Festuca arundinacea	m, r	LC	18.01	2.25	0.05	hemicryptophyte	anemochory	rhizome	–	1
Festuca brevipila	m, r	LC	5.70	0.64	0.04	hemicryptophyte	anemochory	rhizome	–	2
Festuca ovina aggr.	m, r	LC	15.91	0.57	0.13	hemicryptophyte	anemochory	rhizome	high	2
Filipendula ulmaria	m, r	LC	26.29	0.78	0.09	hemicryptophyte	anemochory	rhizome	–	2
Frangula alnus	r	LC	23.29	31.70	0.00	nanophanerophyte	zoochory	root	low	2
Fraxinus excelsior	m	LC	14.30	60.32	0.03	phanerophyte	anemochory	root	medium	2
Fumaria officinalis s.l.	m	LC	29.03	3.20	0.61	therophyte	zoochory	none	–	3
Galeopsis angustifolia	r	LC	18.18	1.87	–	therophyte	zoochory	none	–	1
Galium verum s.l.	m, r	LC	20.65	0.54	0.04	hemicryptophyte	zoochory	rhizome	–	2
Geranium columbinum	m, r	LC	27.45	3.95	0.00	therophyte	autochory	none	–	1
Geranium molle	m, r	LC	25.07	1.10	0.07	therophyte	autochory	none	–	3
Geranium pratense	m	NT	21.04	8.33	0.50	hemicryptophyte	autochory	rhizome	–	2

Geranium purpureum	m, r	LC	–	1.94	–	therophyte	autochory	none	–	3
Geranium pusillum	m, r	LC	25.50	0.81	0.38	therophyte	autochory	none	–	3
Geranium rotundifolium	m, r	LC	33.21	1.81	0.00	therophyte	autochory	none	–	5
Helianthemum nummularium s.l.	m, r	LC	16.68	1.05	0.12	chamaephyte	zoochory	runner	high	1
Helictotrichon pubescens	m	LC	18.51	2.03	–	hemicryptophyte	anemochory	–	–	2
Herniaria glabra	r	LC	21.63	0.08	–	hemicryptophyte	anemochory	none	–	4
Herniaria hirsuta	r	NT	27.63	0.50	0.00	chamaephyte	anemochory	none	–	5
Hieracium caespitosum	m	EN	29.29	0.11	0.00	hemicryptophyte	anemochory	rhizome	–	1
Hieracium glaucinum aggr.	m	LC	18.22	–	–	hemicryptophyte	anemochory	–	–	1
Hieracium lachenalii aggr.	m	LC	–	–	–	hemicryptophyte	anemochory	rhizome	–	2
Hieracium lactucella	r	LC	36.89	–	0.00	hemicryptophyte	anemochory	rhizome	–	1
Hieracium laevigatum aggr.	m	LC	27.85	0.36	0.00	hemicryptophyte	anemochory	rhizome	–	2
Hieracium murorum aggr.	m	LC	40.40	–	–	hemicryptophyte	anemochory	rhizome	–	2
Hieracium pilosella	m, r	LC	17.61	0.21	0.15	hemicryptophyte	anemochory	rhizome	–	2
Hieracium piloselloides aggr.	m, r	LC	21.24	0.67	–	hemicryptophyte	anemochory	rhizome	–	1
Hieracium sabaudum aggr.	r	LC	33.70	0.41	–	hemicryptophyte	anemochory	rhizome	–	2
Himantoglossum hircinum	m	NT	19.99	–	–	geophyte	anemochory	root	–	1
Hippocrepis comosa	m	LC	15.76	3.50	0.21	chamaephyte	anemochory	rhizome	–	1
Hippocrepis emerus	m	LC	–	6.20	–	nanophanerophyte	anemochory	–	–	3
Holcus mollis	r	LC	37.18	0.35	0.03	hemicryptophyte	anemochory	rhizome	–	2
Holosteum umbellatum	r	LC	34.01	0.11	0.00	therophyte	anemochory	none	–	2
Hordeum murinum	m, r	LC	26.35	6.90	0.33	therophyte	anemochory	rhizome	–	4
Humulus lupulus	m, r	LC	33.31	3.38	0.22	hemicryptophyte	anemochory	rhizome	–	3
Hypericum hirsutum	m	LC	29.63	0.10	0.70	hemicryptophyte	anemochory	rhizome	–	1
Hypericum montanum	m	LC	28.75	0.06	1.00	hemicryptophyte	anemochory	runner	–	1
Hypericum perforatum s.l.	m, r	LC	57.18	0.17	0.64	hemicryptophyte	zoochory	root	–	3
Hypochaeris radicata	m	LC	24.97	0.80	0.67	hemicryptophyte	anemochory	–	–	3
Impatiens parviflora	m	–	119.25	7.39	0.00	therophyte	autochory	–	–	2
Inula conyza	m, r	LC	15.70	0.23	0.50	hemicryptophyte	anemochory	rhizome	–	2
Isatis tinctoria	m	LC	18.43	2.51	–	hemicryptophyte	anemochory	root	–	2
Juncus articulatus	r	LC	15.74	0.02	0.91	hemicryptophyte	anemochory	rhizome	low	1
Juncus effusus	r	LC	10.63	0.02	0.93	hemicryptophyte	anemochory	rhizome	medium	2

Knautia arvensis	m	LC	19.36	4.06	0.06	hemicryptophyte	zoochory	rhizome	–	3
Lactuca serriola	r	LC	17.39	0.52	0.22	therophyte	anemochory	none	–	4
Lamium amplexicaule	r	LC	36.67	0.56	0.56	therophyte	zoochory	none	–	3
Lamium galeobdolon ssp. *montanum*	m	LC	–	–	–	chamaephyte	zoochory	–	–	1
Lamium maculatum	m	LC	31.63	1.68	1.00	hemicryptophyte	zoochory	runner	–	2
Lathyrus latifolius	m, r	LC	18.70	51.10	0.00	geophyte	autochory	rhizome	high	4
Lathyrus pratensis	m	LC	26.40	12.02	0.05	geophyte	autochory	rhizome	–	2
Lathyrus sylvestris	m	LC	–	41.51	0.00	geophyte	autochory	rhizome	high	2
Legousia speculum-veneris	r	VU	42.81	0.19	0.00	therophyte	anemochory	none	–	1
Leontodon autumnalis	r	LC	25.84	0.73	0.11	hemicryptophyte	anemochory	rhizome	–	3
Leontodon hispidus	m	LC	25.76	1.11	0.17	hemicryptophyte	anemochory	rhizome	–	2
Lepidium virginicum	m, r	–	22.32	0.47	0.90	hemicryptophyte	hydrochoryy	none	–	5
Leucanthemum ircutianum	m, r	NE	18.61	–	0.00	hemicryptophyte	anemochory	rhizome	–	3
Ligustrum vulgare	m, r	LC	17.66	20.30	0.04	nanophanerophyte	zoochory	–	medium	2
Linaria repens	r	NT	27.56	0.23	0.00	geophyte	anemochory	rhizome	–	2
Linaria vulgaris	m, r	LC	29.87	0.16	0.26	geophyte	anemochory	rhizome	–	3
Linum catharticum	m	LC	31.42	0.15	0.44	therophyte	anemochory	none	–	1
Listera ovata	m	LC	33.50	–	0.00	geophyte	anemochory	rhizome	–	2
Lotus corniculatus	m, r	LC	23.91	1.26	0.15	hemicryptophyte	zoochory	root	medium	3
Lotus pedunculatus	r	LC	29.13	0.72	0.10	hemicryptophyte	autochory	rhizome	–	2
Luzula campestris	m	LC	25.83	0.64	0.40	hemicryptophyte	zoochory	rhizome	–	2
Lycopus europaeus	r	LC	43.63	0.27	0.18	geophyte	hydrochory	bulb&tuber	–	2
Lysimachia nummularia	m	LC	32.36	0.27	0.09	hemicryptophyte	autochory	runner	–	3
Lysimachia vulgaris	m, r	LC	23.52	0.25	0.29	hemicryptophyte	anemochory	rhizome	–	1
Lythrum salicaria	m, r	LC	20.46	0.18	0.36	hemicryptophyte	anemochory	rhizome	–	2
Malva moschata	m, r	LC	18.80	2.30	0.20	hemicryptophyte	anemochory	none	–	4
Malva sylvestris	m, r	LC	25.61	4.59	0.73	hemicryptophyte	anemochory	none	–	4
Matricaria chamomilla	r	LC	–	0.08	0.67	therophyte	anemochory	–	–	3
Medicago falcata	r	NT	–	2.47	–	hemicryptophyte	zoochory	rhizome	–	2
Medicago minima	m, r	LC	25.38	1.10	0.32	hemicryptophyte	zoochory	none	–	1
Medicago sativa	r	LC	21.86	2.24	0.59	hemicryptophyte	zoochory	rhizome	high	3
Medicago x varia	r	–	–	–	–	hemicryptophyte	zoochory	–	–	–

Melica ciliata	r	LC	20.06	0.64	0.00	hemicryptophyte	anemochory	rhizome	–	1
Melilotus albus	m, r	LC	–	2.03	–	hemicryptophyte	anemochory	–	–	3
Melilotus officinalis	m, r	LC	20.01	2.80	0.28	hemicryptophyte	anemochory	none	high	3
Mentha aquatica	m	LC	26.16	0.12	0.52	hemicryptophyte	hydrochory	rhizome	–	1
Mentha longifolia	r	LC	28.43	0.05	–	geophyte	zoochory	rhizome	–	2
Minuartia hybrida	m, r	LC	20.76	0.16	–	therophyte	anemochory	none	–	1
Muscari racemosum	m, r	DD	–	8.80	–	geophyte	anemochory	bulb&tuber	–	4
Mycelis muralis	r	LC	64.45	0.49	0.09	hemicryptophyte	anemochory	root	–	2
Myosotis ramosissima	m, r	NT	28.64	0.22	0.65	therophyte	anemochory	–	–	1
Myosotis scorpioides	m	LC	52.59	0.43	0.18	hemicryptophyte	anemochory	–	low	1
Nymphaea alba	m	NT	11.05	1.94	0.00	hydrophyte	hydrochory	rhizome	–	2
Oenothera biennis aggr.	m, r	–	18.96	0.42	0.56	hemicryptophyte	anemochory	none	medium	4
Oenothera glazioviana	r	–	–	0.62	–	hemicryptophyte	anemochory	–	–	3
Oenothera parviflora aggr.	r	–	17.84	0.58	1.00	hemicryptophyte	anemochory	none	–	4
Onobrychis viciifolia	m, r	–	18.49	18.48	0.00	hemicryptophyte	zoochory	rhizome	medium	1
Ononis repens	m, r	LC	22.97	4.49	0.00	hemicryptophyte	autochory	rhizome	–	1
Onopordum acanthium	r	VU	14.25	7.89	1.00	hemicryptophyte	anemochory	none	–	4
Ophrys apifera	m	VU	19.67	–	–	geophyte	anemochory	root	–	1
Orchis militaris	m	NT	21.53	0.00	–	geophyte	anemochory	root	–	1
Origanum vulgare	m, r	LC	25.72	0.10	0.42	chamaephyte	anemochory	rhizome	–	1
Ornithogalum umbellatum	m	LC	14.08	–	0.00	geophyte	zoochory	bulb&tuber	–	4
Orobanche caryophyllacea	m	LC	–	–	–	geophyte	anemochory	none	–	1
Orobanche minor	m	LC	–	0.02	–	geophyte	anemochory	none	–	1
Papaver argemone	r	VU	23.80	0.16	0.53	therophyte	anemochory	none	–	2
Papaver dubium s.l.	m, r	LC	23.99	0.13	0.44	therophyte	anemochory	–	–	2
Papaver rhoeas	m, r	LC	32.64	0.16	0.63	therophyte	anemochory	none	–	2
Pastinaca sativa	m, r	LC	27.93	3.52	0.31	hemicryptophyte	anemochory	root	–	3
Petrorhagia prolifera	m, r	LC	15.30	0.35	0.00	therophyte	anemochory	none	–	1
Petrorhagia saxifraga	r	LC	–	0.14	–	chamaephyte	anemochory	none	–	1
Phalaris arundinacea	r	LC	23.35	0.65	0.07	geophyte	anemochory	rhizome	low	2
Phragmites australis	m, r	LC	14.56	0.12	0.01	geophyte	anemochory	rhizome	low	2
Phytolacca esculenta	r	–	51.25	–	–	hemicryptophyte	zoochory	–	–	5

Picris hieracioides	m, r	LC	28.98	1.12	0.20	hemicryptophyte	anemochory	root	–	2
Pimpinella major	m, r	LC	26.61	2.07	0.16	hemicryptophyte	anemochory	root	–	1
Pimpinella peregrina	m	–	–	0.50	–	hemicryptophyte	hemerochory	–	–	1
Pimpinella saxifraga	m	LC	17.11	1.15	0.02	hemicryptophyte	anemochory	root	–	1
Pinus sylvestris	m	LC	4.88	7.82	0.00	phanerophyte	anemochory	–	high	1
Plantago arenaria	r	EN	16.28	1.11	1.00	therophyte	zoochory	none	–	3
Plantago major	r	LC	20.69	0.23	0.65	hemicryptophyte	zoochory	rhizome	medium	3
Plantago media	m	LC	18.81	0.36	0.30	hemicryptophyte	zoochory	rhizome	–	2
Poa bulbosa	r	LC	35.59	0.85	0.29	hemicryptophyte	zoochory	rhizome	medium	2
Poa compressa	m, r	LC	18.24	0.21	0.48	hemicryptophyte	anemochory	rhizome	medium	3
Poa nemoralis	m, r	LC	34.68	0.30	0.39	hemicryptophyte	anemochory	rhizome	–	3
Polygala amarella	m	LC	20.79	0.82	0.07	hemicryptophyte	zoochory	none	–	1
Polygonatum multiflorum	m	LC	42.98	24.08	0.00	geophyte	zoochory	rhizome	–	2
Populus alba	r	LC	11.70	0.12	–	phanerophyte	anemochory	root	medium	3
Populus tremula	m	LC	15.65	0.26	0.00	phanerophyte	anemochory	root	medium	2
Portulaca oleracea	r	LC	20.02	0.24	0.86	therophyte	anemochory	none	–	5
Potentilla anserina	m	LC	20.90	0.90	0.18	hemicryptophyte	zoochory	runner	–	3
Potentilla argentea	m, r	LC	15.99	0.09	0.60	hemicryptophyte	anemochory	root	–	2
Potentilla erecta	m	LC	25.38	0.47	0.37	hemicryptophyte	zoochory	rhizome	–	1
Potentilla inclinata	r	EN	13.13	0.31	–	hemicryptophyte	anemochory	root	–	1
Potentilla neumanniana	m, r	LC	15.39	0.92	–	chamaephyte	zoochory	root	–	3
Potentilla recta	m, r	LC	15.90	0.30	0.20	hemicryptophyte	zoochory	rhizome	–	2
Potentilla sterilis	m	LC	24.60	0.53	0.42	hemicryptophyte	zoochory	runner	–	1
Primula veris s.l.	m	LC	19.32	0.82	0.06	hemicryptophyte	anemochory	rhizome	–	2
Prunella grandiflora	m	LC	17.45	1.19	0.18	hemicryptophyte	hydrochory	rhizome	–	1
Prunella vulgaris	m	LC	28.63	2.70	0.20	hemicryptophyte	hydrochory	runner	medium	2
Prunus avium	m, r	LC	16.08	209.98	0.00	phanerophyte	zoochory	–	medium	2
Prunus mahaleb	m, r	LC	16.81	83.74	–	nanophanerophyte	zoochory	–	high	3
Prunus padus	m	LC	21.00	139.50	0.23	nanophanerophyte	zoochory	–	low	2
Prunus spinosa	m, r	LC	17.10	203.47	0.00	nanophanerophyte	zoochory	root	medium	2
Quercus robur	m	LC	11.36	3084.22	0.00	phanerophyte	zoochory	root	medium	2
Ranunculus bulbosus	m	LC	19.42	2.72	0.37	hemicryptophyte	anemochory	bulb&tuber	–	2

Raphanus raphanistrum	r	LC	27.88	19.12	0.33	therophyte	zoochory	none	–	2
Reseda lutea	m, r	LC	17.93	0.72	0.91	hemicryptophyte	anemochory	root	–	3
Rhamnus cathartica	m	LC	19.07	25.89	–	nanophanerophyte	zoochory	root	medium	1
Rhinanthus alectorolophus	m, r	LC	20.42	3.25	0.60	therophyte	anemochory	none	–	1
Rhinanthus minor	m	LC	19.35	2.51	0.22	therophyte	anemochory	none	–	1
Ribes rubrum	m	–	31.45	5.12	0.00	nanophanerophyte	zoochory	–	low	2
Robinia pseudoacacia	r	–	34.62	19.43	1.00	phanerophyte	anemochory	root	high	3
Rorippa sylvestris	r	LC	31.97	0.14	0.27	hemicryptophyte	anemochory	rhizome	low	1
Rosa agrestis	m	NT	11.28	18.87	–	nanophanerophyte	zoochory	–	high	2
Rosa arvensis	m	LC	28.58	13.53	0.00	nanophanerophyte	zoochory	–	medium	1
Rosa canina	m, r	LC	16.21	114.67	0.03	nanophanerophyte	zoochory	–	high	2
Rosa corymbifera	m, r	LC	–	–	0.00	nanophanerophyte	zoochory	–	high	2
Rosa rubiginosa	m	NT	12.23	14.95	0.00	nanophanerophyte	zoochory	–	high	1
Rosa tomentosa aggr.	m	LC	–	10.60	0.00	nanophanerophyte	zoochory	–	high	1
Rubus armeniacus	m, r	–	–	–	–	hemicryptophyte	zoochory	–	–	4
Rubus fruticosus aggr.	m	LC	19.14	2.55	0.55	hemicryptophyte	zoochory	root	–	–
Rumex acetosa	m	LC	28.06	0.78	0.24	hemicryptophyte	anemochory	rhizome	–	2
Rumex acetosella	m	LC	22.73	0.57	0.70	hemicryptophyte	anemochory	rhizome	–	2
Rumex crispus	m	LC	26.34	1.85	0.31	hemicryptophyte	anemochory	rhizome	–	3
Rumex thyrsiflorus	m, r	NT	21.39	0.71	0.00	hemicryptophyte	anemochory	rhizome	–	3
Sagina apetala s.l.	r	LC	21.17	0.01	0.70	therophyte	anemochory	–	–	2
Sagina procumbens	r	LC	19.80	0.02	0.82	chamaephyte	anemochory	runner	–	4
Salix alba	m, r	LC	12.11	0.12	0.44	phanerophyte	anemochory	–	low	2
Salix caprea	m, r	LC	21.14	0.09	0.02	nanophanerophyte	anemochory	–	medium	3
Salix cinerea	m, r	LC	11.57	0.07	0.00	nanophanerophyte	anemochory	root	low	2
Salix elaeagnos	m, r	LC	–	0.25	–	nanophanerophyte	anemochory	–	low	2
Salix purpurea	r	LC	11.15	0.09	0.00	nanophanerophyte	anemochory	–	low	1
Salix viminalis	r	LC	13.89	–	0.00	nanophanerophyte	anemochory	–	low	2
Salix x rubens	m, r	–	–	–	–	nanophanerophyte	anemochory	–	–	–
Salvia pratensis	m, r	LC	25.48	2.39	0.10	hemicryptophyte	zoochory	rhizome	–	2
Sambucus nigra	m, r	LC	24.47	25.58	0.23	nanophanerophyte	zoochory	runner	medium	3
Sanguisorba minor s.l.	m, r	LC	18.33	6.18	0.13	hemicryptophyte	anemochory	rhizome	low	2

Saponaria officinalis	m, r	LC	24.80	1.56	0.00	hemicryptophyte	anemochory	rhizome	–	4
Saxifraga tridactylites	m, r	LC	28.77	0.01	0.29	therophyte	anemochory	none	–	1
Scabiosa columbaria	m, r	LC	20.04	1.90	0.17	hemicryptophyte	anemochory	rhizome	–	1
Schoenoplectus lacustris	m	LC	–	1.94	0.00	geophyte	zoochory	rhizome	–	1
Scrophularia canina	r	NT	17.17	0.59	–	hemicryptophyte	anemochory	rhizome	–	3
Scrophularia nodosa	m	LC	39.65	0.17	0.89	hemicryptophyte	anemochory	rhizome	–	2
Scrophularia umbrosa	r	LC	32.02	0.08	1.00	hemicryptophyte	anemochory	rhizome	–	1
Securigera varia	m, r	LC	–	3.32	0.00	hemicryptophyte	anemochory	–	–	2
Sedum acre	m, r	LC	13.97	0.04	0.36	chamaephyte	anemochory	runner	–	3
Sedum album	m, r	LC	16.17	0.03	–	chamaephyte	anemochory	runner	–	2
Sedum maximum	m	LC	–	0.05	–	hemicryptophyte	anemochory	rhizome	–	2
Sedum rupestre	m, r	LC	13.95	0.05	0.00	chamaephyte	anemochory	–	–	2
Sedum sexangulare	m, r	LC	13.64	0.03	0.75	chamaephyte	anemochory	rhizome	–	2
Senecio aquaticus	m	NT	25.61	0.34	0.00	hemicryptophyte	anemochory	rhizome	–	1
Senecio erucifolius	m, r	LC	14.38	0.31	0.05	hemicryptophyte	anemochory	rhizome	–	1
Senecio inaequidens	m, r	–	19.42	0.25	–	chamaephyte	anemochory	–	–	5
Senecio viscosus	r	LC	22.47	0.51	0.80	therophyte	anemochory	none	–	3
Sherardia arvensis	m	LC	22.47	1.66	0.25	therophyte	zoochory	none	–	1
Silene flos-cuculi	m, r	LC	–	0.15	0.67	hemicryptophyte	anemochory	–	–	2
Silene nutans	m	LC	21.72	0.38	0.46	hemicryptophyte	anemochory	rhizome	–	2
Silene pratensis	m, r	LC	–	–	–	hemicryptophyte	anemochory	runner	–	4
Silene vulgaris	m, r	LC	23.53	1.25	0.45	hemicryptophyte	anemochory	runner	–	2
Sisymbrium officinale	m, r	LC	26.72	0.28	0.42	therophyte	anemochory	none	–	3
Sisymbrium orientale	r	–	22.33	0.25	–	therophyte	anemochory	none	–	2
Solanum dulcamara	r	LC	41.11	27.59	0.26	chamaephyte	zoochory	root	–	3
Solidago virgaurea	m	LC	29.97	0.61	0.13	hemicryptophyte	anemochory	rhizome	–	2
Sonchus arvensis	r	LC	21.32	0.74	0.77	hemicryptophyte	anemochory	rhizome	–	2
Sorbus aucuparia	m	LC	15.82	62.42	0.04	nanophanerophyte	zoochory	root	medium	2
Stachys officinalis	m	LC	24.23	6.37	0.29	hemicryptophyte	anemochory	–	–	2
Stachys recta	m, r	LC	22.12	1.42	0.08	hemicryptophyte	zoochory	rhizome	–	1
Stachys sylvatica	m	LC	50.77	1.39	0.33	hemicryptophyte	zoochory	rhizome	–	2
Stellaria graminea	m	LC	33.56	0.28	0.29	hemicryptophyte	autochory	rhizome	–	2

Stellaria holostea	m	NT	30.98	2.78	0.09	chamaephyte	anemochory	rhizome	–	2
Stellaria pallida	r	LC	59.54	0.13	–	therophyte	autochory	none	–	1
Tanacetum vulgare	m, r	LC	20.38	0.19	0.19	hemicryptophyte	anemochory	rhizome	–	4
Taraxacum laevigatum aggr.	m, r	LC	50.40	0.43	–	hemicryptophyte	anemochory	rhizome	–	4
Teucrium botrys	r	VU	39.20	1.14	1.00	therophyte	zoochory	none	–	1
Teucrium scorodonia	r	LC	32.47	0.96	0.42	hemicryptophyte	zoochory	rhizome	–	2
Thlaspi arvense	r	LC	23.76	1.08	0.87	therophyte	zoochory	none	–	3
Thlaspi perfoliatum	m, r	LC	23.76	1.08	0.87	therophyte	hydrochory	none	–	1
Thymus pulegioides s.l.	m, r	LC	25.88	0.16	0.38	chamaephyte	anemochory	rhizome	–	2
Tilia cordata	m	LC	22.48	41.82	0.08	phanerophyte	anemochory	root	medium	2
Torilis arvensis	m	NT	28.04	1.90	–	therophyte	zoochory	none	–	1
Torilis japonica	m	LC	26.93	1.88	0.49	hemicryptophyte	zoochory	none	–	2
Tragopogon dubius	m, r	LC	25.38	8.59	0.75	hemicryptophyte	anemochory	none	high	2
Tragopogon pratensis ssp. *orientalis*	m	LC	25.17	8.36	0.13	hemicryptophyte	anemochory	none	–	2
Trifolium arvense	m, r	LC	19.55	0.50	0.50	therophyte	anemochory	none	–	2
Trifolium campestre	m, r	LC	33.48	0.29	0.21	therophyte	anemochory	none	–	2
Trifolium medium	m	LC	18.10	2.04	0.00	hemicryptophyte	anemochory	rhizome	–	1
Trisetum flavescens	m	LC	25.62	0.31	0.02	hemicryptophyte	anemochory	rhizome	–	2
Turritis glabra	m	LC	–	0.05	–	hemicryptophyte	anemochory	–	–	2
Typha latifolia	m	LC	10.97	0.09	0.59	geophyte	anemochory	rhizome	low	2
Ulmus glabra	m	LC	23.80	11.30	0.00	phanerophyte	anemochory	root	medium	2
Ulmus laevis	m, r	EN	37.44	7.32	–	phanerophyte	anemochory	root	low	2
Ulmus minor	m, r	LC	20.04	7.39	0.00	phanerophyte	anemochory	root	medium	2
Valeriana officinalis s.l.	m	LC	29.86	1.11	0.00	hemicryptophyte	anemochory	rhizome	–	2
Valeriana wallrothii	m	NT	29.86	1.11	0.00	hemicryptophyte	anemochory	rhizome	–	2
Valerianella carinata	m, r	LC	32.97	0.52	0.22	therophyte	anemochory	none	–	2
Valerianella locusta	m, r	LC	33.67	1.32	0.09	therophyte	anemochory	none	–	2
Valerianella rimosa	r	EN	33.11	1.34	0.00	therophyte	anemochory	none	–	2
Verbascum densiflorum	m, r	LC	17.57	0.10	0.75	hemicryptophyte	anemochory	none	–	2
Verbascum lychnitis	m, r	LC	16.85	0.12	0.40	hemicryptophyte	anemochory	none	–	2
Verbascum nigrum	m, r	LC	18.70	0.12	0.58	hemicryptophyte	anemochory	none	–	2
Verbascum phlomoides	m, r	NT	18.37	0.14	0.67	hemicryptophyte	anemochory	none	–	2

Verbascum pulverulentum	m, r	EN	20.10	0.17	–	hemicryptophyte	anemochory	none	–	2
Verbascum thapsus	m, r	LC	18.61	0.09	0.68	hemicryptophyte	anemochory	none	–	2
Verbena officinalis	m, r	LC	14.52	0.36	0.50	hemicryptophyte	zoochory	none	–	4
Veronica beccabunga	r	LC	72.42	0.30	0.72	hemicryptophyte	hydrochory	runner	–	1
Veronica officinalis	m	LC	25.77	0.18	0.63	chamaephyte	hydrochory	rhizome	–	1
Veronica teucrium	m	LC	–	0.20	–	chamaephyte	anemochory	rhizome	–	2
Veronica triphyllos	r	VU	36.38	0.40	0.00	therophyte	anemochory	none	–	2
Viburnum lantana	m	LC	18.68	40.33	0.00	nanophanerophyte	zoochory	root	medium	1
Viburnum opulus	m	LC	23.43	52.53	0.00	nanophanerophyte	zoochory	root	medium	2
Vicia angustifolia s.l.	m, r	LC	–	19.79	–	hemicryptophyte	autochory	none	–	2
Vicia cracca	m, r	LC	24.40	15.61	0.05	hemicryptophyte	autochory	rhizome	high	2
Vicia hirsuta	m, r	LC	20.21	6.06	0.25	therophyte	autochory	none	–	2
Vicia sativa aggr.	m, r	LC	21.32	27.59	0.23	therophyte	autochory	rhizome	low	2
Vicia tetrasperma	m, r	NT	29.92	3.78	0.21	therophyte	autochory	none	–	2
Viola alba	m	LC	23.44	1.88	–	hemicryptophyte	zoochory	rhizome	–	1
Viola hirta	m	LC	21.11	3.17	0.06	hemicryptophyte	zoochory	rhizome	–	2
Viola odorata	m, r	LC	23.33	3.43	1.00	hemicryptophyte	zoochory	rhizome	–	2
Vulpia myuros	m, r	LC	13.30	0.49	0.25	therophyte	anemochory	rhizome	high	1

b) Orthoptera

Species	Habitat type	Red List	Suborder	Body size (mm)	Dispersal ability	Food specialisation
Barbitistes serricauda	m	LC	Ensifera	19.00	low	forbivorous
Calliptamus italicus	r	VU	Caelifera	23.75	moderate	forbivorous
Chorthippus biguttulus	m, r	LC	Caelifera	16.50	high	graminivorous
Chorthippus brunneus	r	LC	Caelifera	18.25	high	graminivorous
Chorthippus dorsatus	m, r	LC	Caelifera	19.00	high	graminivorous
Chrysochraon dispar	m, r	NT	Caelifera	21.25	moderate	herbivorous
Conocephalus fuscus	m, r	VU	Ensifera	15.25	high	omnivorous
Eumodicogryllus bordigalensis	r	NT	Ensifera	12.63	moderate	omnivorous
Gomphocerippus rufus	m, r	LC	Caelifera	17.50	moderate	graminivorous
Gryllus campestris	m	LC	Ensifera	22.50	low	omnivorous
Leptophyes punctatissima	m, r	LC	Ensifera	13.50	low	forbivorous
Meconema meridionale	m, r	LC	Ensifera	13.00	low	insectivorous
Mecostethus parapleurus	m	LC	Caelifera	22.75	moderate	graminivorous
Metrioptera bicolor	m, r	VU	Ensifera	16.00	moderate	omnivorous
Metrioptera roeselii	m, r	LC	Ensifera	17.25	moderate	graminivorous
Nemobius sylvestris	m	LC	Ensifera	9.25	low	forbivorous
Oecanthus pellucens	m, r	LC	Ensifera	14.25	high	omnivorous
Oedipoda caerulescens	m, r	NT	Caelifera	21.50	high	herbivorous
Omocestus rufipes	m	NT	Caelifera	17.00	low	graminivorous
Phaneroptera falcata	m, r	VU	Ensifera	15.50	high	forbivorous
Phaneroptera nana	m, r	LC	Ensifera	15.00	high	forbivorous
Pholidoptera griseoaptera	m, r	LC	Ensifera	17.75	low	omnivorous
Platycleis albopunctata	m, r	NT	Ensifera	20.75	moderate	herbivorous
Sphingonotus caerulans	r	VU	Caelifera	22.75	high	herbivorous
Stethophyma grossum	m	VU	Caelifera	22.25	moderate	graminivorous

Red List: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered

c) Lepidoptera

Species	**Habitat type**	**Red List**	**Wing length (mm)**	**Dispersal ability**	**Food specialisation***
Anthocharis cardamines	m, r	LC	22.0	moderate	o2+
Aphantopus hyperantus	m, r	LC	20.0	low	p
Araschnia levana	m	LC	18.5	moderate	o2
Aricia agestis	r	LC	14.0	moderate	p
Carcharodus alceae	m, r	NT	14.0	moderate	o2
Carterocephalus palaemon	m	LC	14.5	low	o2+
Celastrina argiolus	m	LC	17.0	moderate	p
Coenonympha pamphilus	m, r	LC	15.0	low	o2+
Colias alfacariensis	r	LC	24.0	high	o2
Colias croceus	m, r	LC	26.0	high	o2+
Colias hyale	m, r	LC	23.0	moderate	p
Cupido argiades	m, r	NT	13.5	moderate	o2+
Erynnis tages	m, r	LC	13.0	low	o2+
Glaucopsyche alexis	r	VU	17.5	low	o2+
Gonepteryx rhamni	m, r	LC	28.0	high	o2
Inachis io	m, r	LC	30.0	high	m
Lasiommata megera	m, r	LC	23.0	moderate	o2+
Leptidea reali/sinapis aggr.	m, r	LC	22.0	moderate	o2+
Lycaena phlaeas	m, r	LC	13.5	moderate	o2
Lycaena tityrus	m	LC	15.0	low	o2
Maniola jurtina	m, r	LC	23.0	moderate	p
Melanargia galathea	m, r	LC	26.0	low	o2+
Ochlodes sylvanus	m, r	LC	15.0	moderate	o2+
Papilio machaon	m, r	LC	38.0	high	o2+
Pararge aegeria	m	LC	22.0	moderate	o2+
Pieris brassicae	m, r	LC	31.0	high	o2+
Pieris napi	m	LC	24.5	high	o2+
Pieris rapae	m, r	LC	27.0	high	o2+

Plebejus argyrognomon	r	EN	16.0	low	o2+
Polyommatus icarus	m, r	LC	16.0	moderate	o2+
Polyommatus semiargus	m, r	LC	16.5	low	o2+
Pyrgus armoricanus	m	NT	13.5	moderate	o2+
Pyrgus malvae	m	LC	13.0	low	o2+
Satyrium pruni	m	VU	15.0	–	o2
Spialia sertorius	m, r	NT	12.0	low	m
Thecla betulae	m	LC	19.0	moderate	o2
Thymelicus acteon	m	EN	13.0	moderate	o2+
Thymelicus sylvestris	m	LC	14.5	low	o2+
Vanessa atalanta	m, r	LC	29.0	high	m
Vanessa cardui	m, r	LC	28.0	high	p
Zygaena ephialtes	r	VU	16.0	–	o2+
Zygaena filipendulae	m, r	LC	16.0	–	o2+
Zygaena loti	m, r	LC	13.5	–	o2+
Zygaena transalpina	r	LC	18.5	–	o2+

Red List: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered

* Food specialisation: m = monophagy, o2 = narrow oligophagy, o2+ = broad oligophagy, p = polyphagy

Table S3 Linear regressions testing the effect of habitat size on total species richness of vascular plants, Orthoptera, and Lepidoptera based on log-transformed data of both species number and area

Taxonomic group	Meadows						Ruderal sites					
	N	R^2	Parameter	SE	Student's *t*	*P*	*N*	R^2	Parameter	SE	Student's *t*	*P*
Vascular plants	60	0.009					28	0.297				
Intercept			2.70	0.42	6.45	**<0.001**			1.64	0.55	2.96	**0.006**
ln(area)			0.06	0.05	1.24	0.22			0.22	0.06	3.52	**0.002**
Orthoptera	58	0.063					25	0.063				
Intercept			0.32	0.61	0.54	0.60			0.24	0.83	0.28	0.78
ln(area)			0.16	0.07	2.21	**0.032**			0.15	0.09	1.62	0.12
Lepidoptera	52	0.175					19	0.047				
Intercept			–0.77	0.75	–1.02	0.31			2.32	1.68	1.38	0.19
ln(area)			0.30	0.09	3.43	**0.001**			–0.09	0.20	–0.44	0.67

Significant *P* values (<0.05) are in bold

N: number of habitat sites

Table S4 Linear regressions (species richness: untransformed; area: log-transformed) testing the effect of habitat size on total species richness of vascular plants, Orthoptera and Lepidoptera

Taxonomic group	Meadows						Ruderal sites					
	N	R^2	Parameter	SE	Student's *t*	*P*	*N*	R^2	Parameter	SE	Student's *t*	*P*
Vascular plants	60	0.007					28	0.393				
Intercept			14.00	10.67	1.31	0.20			–31.06	16.23	–1.91	0.07
ln(area)			1.55	1.30	1.19	0.24			7.88	1.83	4.30	**<0.001**
Orthoptera	58	0.140					25	0.142				
Intercept			–3.24	2.91	–1.11	0.27			–3.32	3.93	–0.84	0.41
ln(area)			1.13	0.35	3.21	**0.002**			1.00	0.45	2.23	**0.036**
Lepidoptera	52	0.173					19	–0.054				
Intercept			–6.70	4.06	–1.65	0.11			3.91	8.91	0.44	0.67
ln(area)			1.63	0.48	3.42	**0.001**			0.29	1.05	0.27	0.79

Significant *P* values (<0.05) are in bold
N: number of habitat sites

Table S5 Summary of the results of the *envfit*-function examining the effects of the size and perimeter-area ratio of a habitat and the percentage cover of various landscape elements in the closer surrounding (r = 200 m) on the species composition of (a) vascular plants, (b) Orthoptera and (c) Lepidoptera in both meadows and ruderal sites

	Meadows			Ruderal sites		
		R^2	P		R^2	P
a) Vascular plants	*N*=60			*N*=28		
Habitat size		0.015	0.687		0.466	**0.002**
Perimeter/area ratio		0.157	**0.010**		0.567	**0.001**
Percentage cover of						
sealed area		0.161	**0.005**		0.028	0.713
agricultural area		0.058	0.199		0.036	0.664
ruderal area		0.062	0.156		0.525	**0.001**
urban green space		0.082	0.083		0.373	**0.004**
forest		0.215	**0.005**		0.040	0.617
water surface area		0.152	**0.018**		0.495	**0.001**
b) Orthoptera	*N*=58			*N*=25		
Habitat size		0.303	**0.001**		0.419	**0.005**
Perimeter/area ratio		0.303	**0.001**		0.261	**0.035**
Percentage cover of						
sealed area		0.529	**0.001**		0.001	0.992
agricultural area		0.660	**0.001**		0.246	**0.047**
ruderal area		0.084	0.073		0.602	**0.001**
urban green space		0.523	**0.001**		0.189	0.084
forest		0.127	**0.027**		0.055	0.536
water surface area		0.010	0.773		0.052	0.553
c) Lepidoptera	*N*=52			*N*=19		
Habitat size		0.223	**0.002**		0.059	0.641
Perimeter/area ratio		0.204	**0.003**		0.100	0.422
Percentage cover of						
sealed area		0.439	**0.001**		0.162	0.259
agricultural area		0.272	**0.001**		0.137	0.325
ruderal area		0.033	0.460		0.669	**0.001**
urban green space		0.136	**0.038**		0.283	0.080
forest		0.178	**0.006**		0.344	**0.042**
water surface area		0.025	0.563		0.105	0.365

Significant *P* values (<0.05) are in bold

N: number of habitat sites

Fig. S1 Species-area relationships (untransformed species richness, log-transformed area) of vascular plants, Orthoptera and Lepidoptera in meadows and ruderal sites

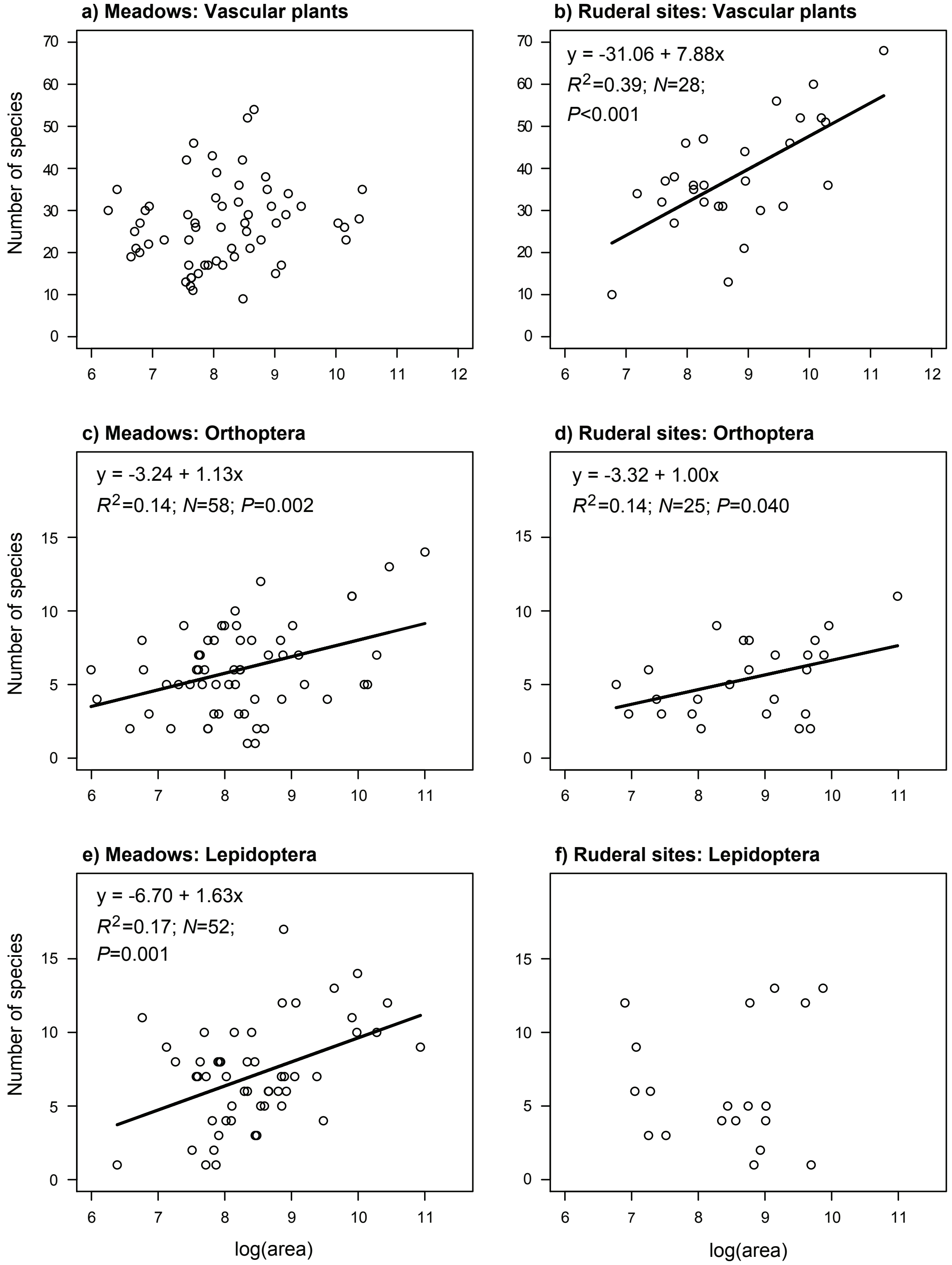
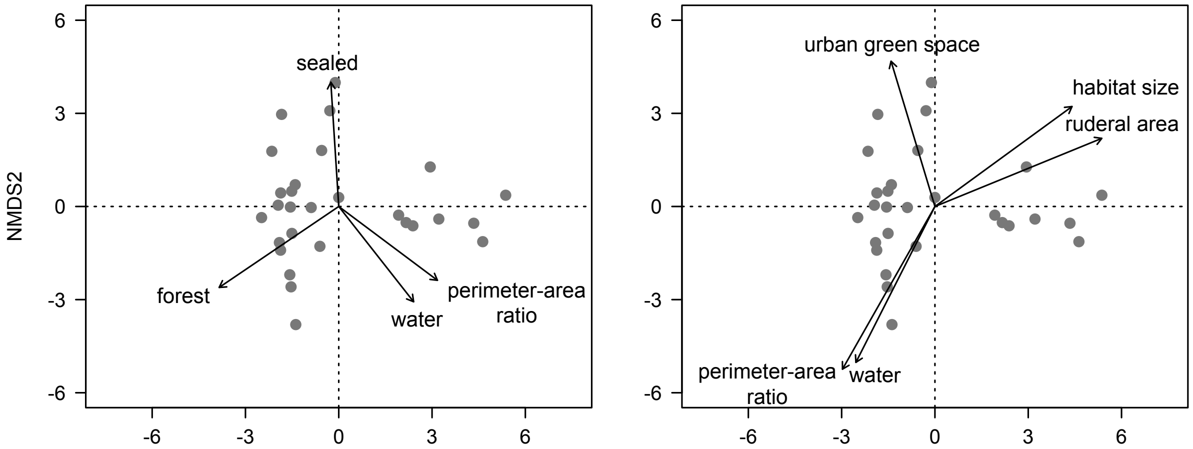
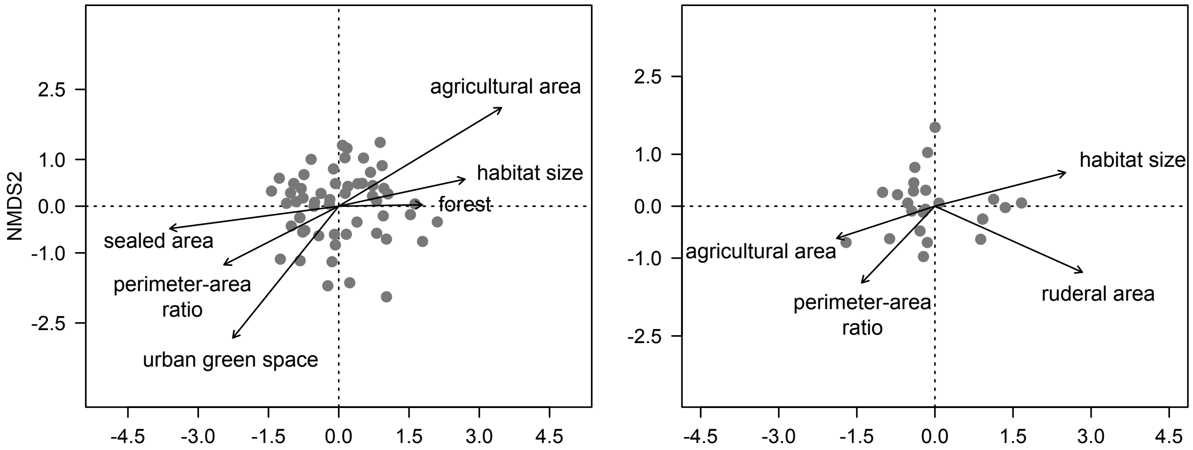


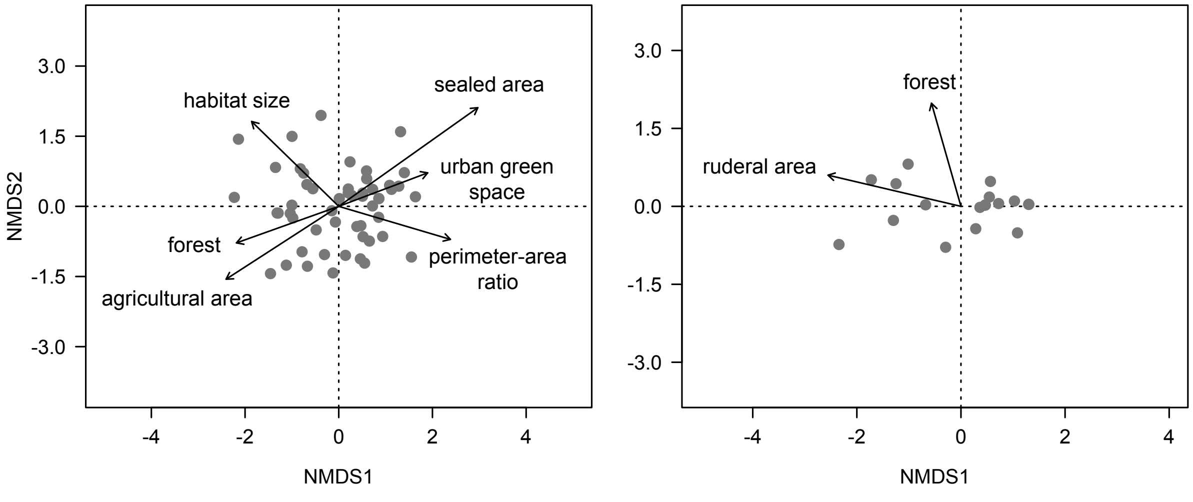
Fig. S2 NMDS ordination diagram based on Euclidean dissimilarities in (a, b) plant, (c, d) Orthoptera and (e, f) Lepidoptera species composition in meadows and ruderal sites. Significant landscape features affecting species composition are shown


a) Meadows: Plants

b) Ruderal sites: Plants

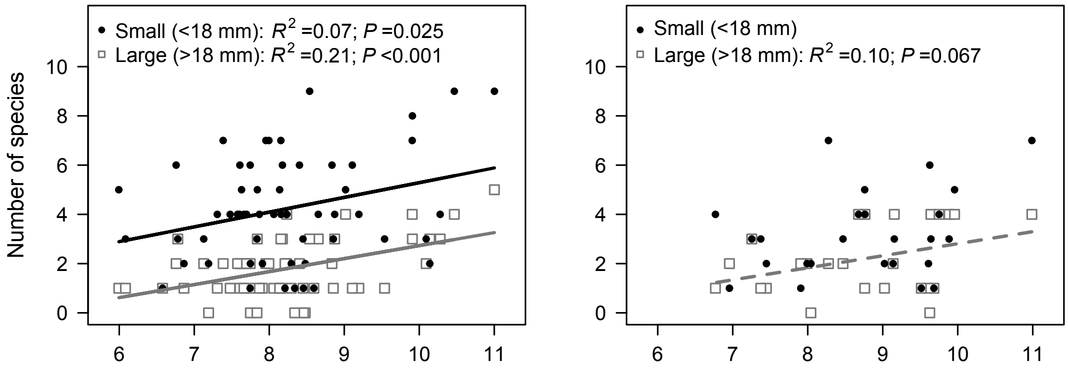

c) Meadows: Orthoptera

d) Ruderal sites: Orthoptera


e) Meadows: Lepidoptera

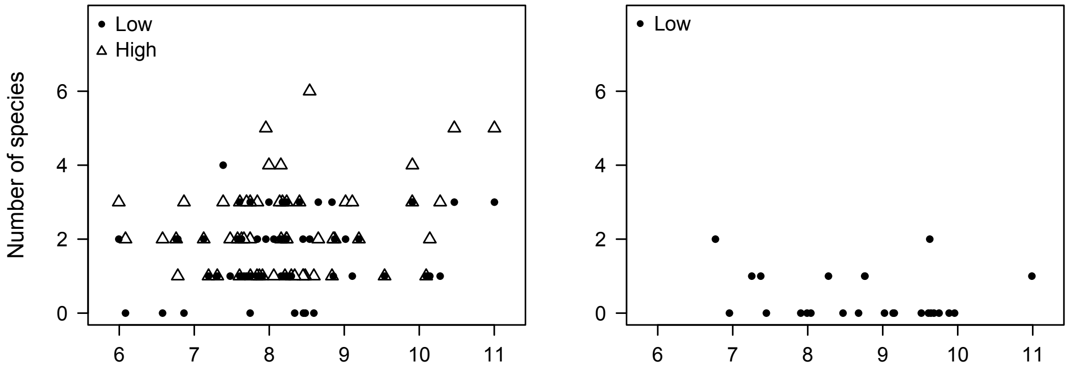
f) Ruderal sites: Lepidoptera

Fig. S3 Relationships between traits of orthopteran species and habitat size in meadows (*N*=58) and ruderal sites (*N*=25): body size, dispersal ability and food specialisation. Adjusted R^2-values and *P*-values are shown for significant effects obtained with the main model (Table 3)



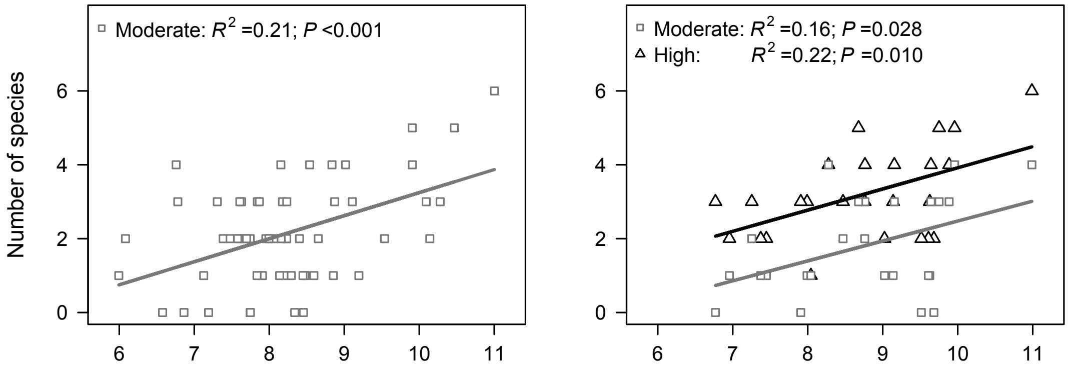
a) Meadows: Body size

b) Ruderal sites: Body size



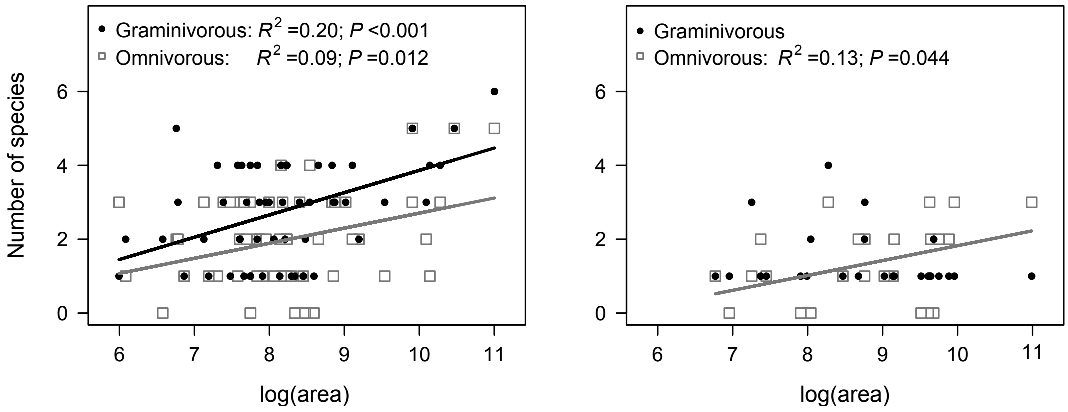
c) Meadows: Dispersal ability

d) Ruderal sites: Dispersal ability



c) Meadows: Dispersal ability

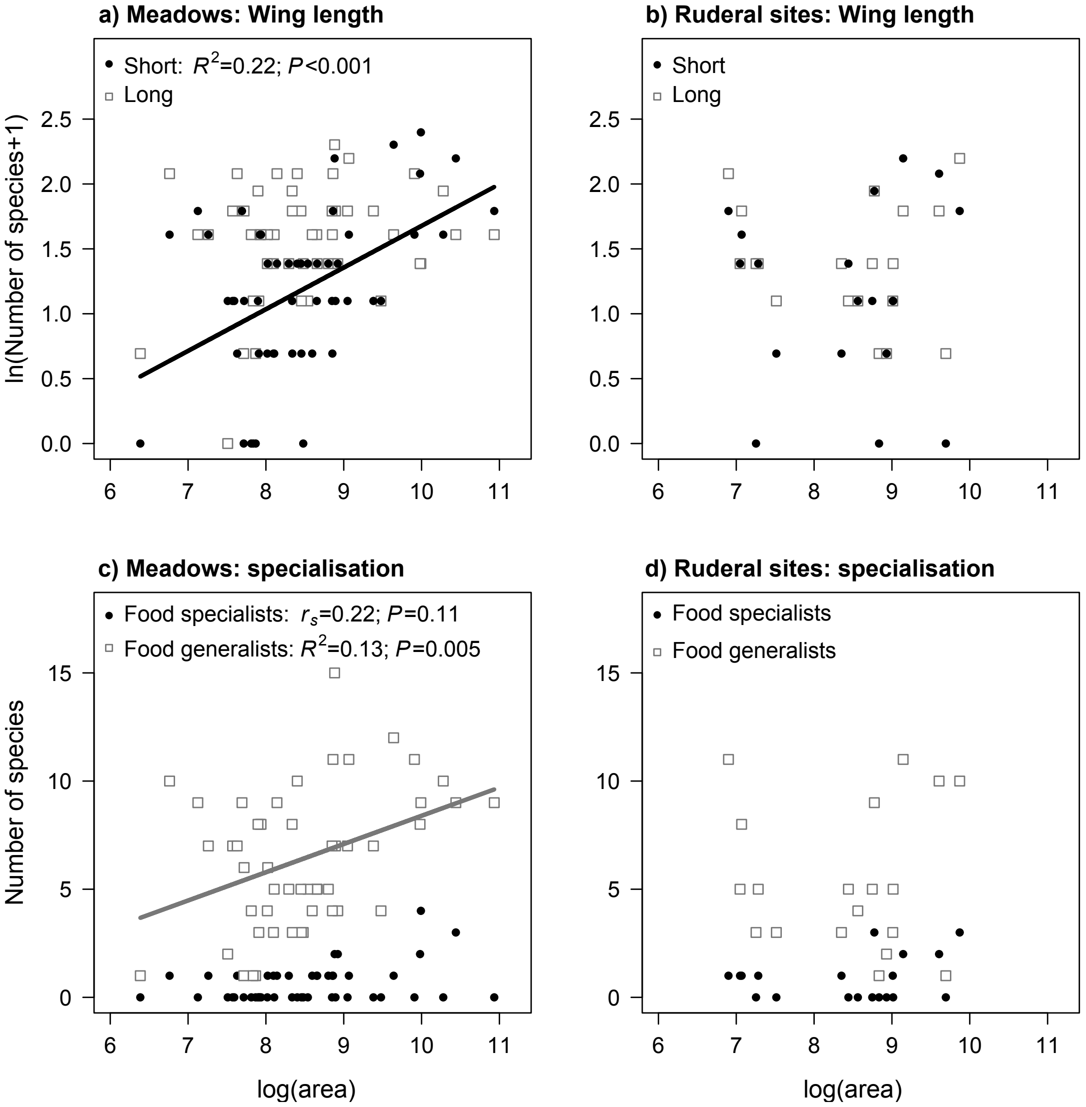
d) Ruderal sites: Dispersal ability



e) Meadows: Food specialisation

f) Ruderal sites: Food specialisation

Fig. S4 Relationships between traits of Lepidoptera species and habitat size in meadows (*N*=52) and ruderal sites (*N*=19): wing length and food specialisation. Adjusted R^2-values and Spearman's rank correlation coefficients (r_s), respectively, and *P*-values are shown for significant effects obtained with the main model (Table 3)



Chapter II

Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders

Ramona L. Melliger, Brigitte Braschler, Hans-Peter Rusterholz, Bruno Baur

PLoS One, 2018, 13(6): e0199245

PLOS ONE

RESEARCH ARTICLE

Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders

Ramona Laila Melliger, Brigitte Braschler*, Hans-Peter Rusterholz, Bruno Baur

Section of Conservation Biology, Department of Environmental Sciences, University of Basel, Basel, Switzerland

* brigitte.braschler@unibas.ch

Abstract

Urbanisation is increasing worldwide and is regarded a major driver of environmental change altering local species assemblages in urban green areas. Forests are one of the most frequent habitat types in urban landscapes harbouring many native species and providing important ecosystem services. By using a multi-taxa approach covering a range of trophic ranks, we examined the influence of degree of urbanisation and forest size on the species richness and functional diversity of plants, and ground surface-active ants and spiders. We conducted field surveys in twenty-six forests in the urban region of Basel, Switzerland. We found that a species' response to urbanisation varied depending on trophic rank, habitat specificity and the diversity indices used. In plants, species richness decreased with degree of urbanisation, whereas that of both arthropod groups was not affected. However, ants and spiders at higher trophic rank showed greater shifts in species composition with increasing degree of urbanisation, and the percentage of forest specialists in both arthropod groups increased with forest size. Local abiotic site characteristics were also crucial for plant species diversity and species composition, while the structural diversity of both leaf litter and vegetation was important for the diversity of ants and spiders. Our results highlight that even small urban forests can harbour a considerable biodiversity including habitat specialists. Nonetheless, urbanisation directly and indirectly caused major shifts in species composition. Therefore, special consideration needs to be given to vulnerable species, including those with special habitat requirements. Locally adapted management practices could be a step forward to enhance habitat quality in a way to maximize diversity of forest species and thus ensure forest ecosystem functioning; albeit large-scale factors also remain important.

Citation: Melliger RL, Braschler B, Rusterholz H-P, Baur B (2018) Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. PLoS ONE 13(6): e0199245. https://doi.org/10.1371/journal.pone.0199245

Editor: Petr Heneberg, Charles University, CZECH REPUBLIC

Received: November 13, 2017

Accepted: April 23, 2018

Published: June 19, 2018

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: Stadtgärtnerei Basel (BBaur), Stiftung Emilia Guggenheim-Schnurr (BBraschler), and Basler Stiftung für biologische Forschung (BBraschler) provided funding for the research. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Urbanisation is increasing globally and is considered a main driver of environmental change [1]. Urbanisation-related factors including reduced habitat size and increased spatial isolation change the dynamics of plant and animal populations in urban green areas [2, 3]. Several studies along urbanisation gradients also reported alterations in abiotic conditions in the remaining habitat patches caused by increases in temperature, precipitation and N deposition from the rural surroundings to the city centre [1, 4, 5]. These changes influence habitat quality and, consequently, the species richness, species composition and functional diversity of plants and animals [3, 6, 7], which in turn affect the functioning of ecosystems [8]. Furthermore, urbanisation can influence the population dynamics of animals and plants by altering the biology of hosts, pathogens and vectors [9]. Although urbanisation frequently reduces the abundance of many parasites and pathogens [10], transmission may also increase among urban-adapted hosts [9]. In some cases, invertebrates can serve as vectors of pathogens which otherwise are absent from urban environments [11]. Finally, plants and animals may be exposed to other chemicals (herbicides, fungicides, pesticides) and other types of pollution in urban environments than in rural agricultural landscapes [9]. Nonetheless, urban areas can harbour remarkably high species richness [12], in some cases exceeding that of their rural surroundings [6, 13].

Forests represent one of the most frequent types of green area in cities [14]. Urban forests provide a wide range of ecosystem functions including habitat for native species and recreation for residents [15, 16]. Both forests and orchards in cities can serve as refugia for rare and threatened specialist species and thus can be of high conservation value [12, 17]. Within urban landscapes, forest sites differ substantially in site history, management and disturbance intensity and consequently in species composition [3, 4, 17, 18]. Urban forests can be remnants of former continuous forests, a result of ongoing succession or actively planted [4]. They can include urban orchards, cemeteries overgrown by trees, or parks [4, 17, 18].

Not all species respond to environmental changes caused by urbanisation in the same way, because they have different requirements regarding their habitat and its surrounding landscape [7, 12, 19]. For example, specialist species may perceive the surrounding matrix as a stronger barrier than generalists, which are able to exploit a wide variety of resources from neighbouring green areas [1, 16, 20]. Thus, specialist species become frequently replaced by generalists [21, 22]. As a result, species composition in urban areas becomes more and more similar, which in turn may lead to a decrease in functional diversity–also called functional homogenisation ([20] and references within). Furthermore, groups of species at high trophic ranks such as herbivores and predators might also be more influenced by increased isolation and habitat loss because of their dependence on other species compared to groups of species at low trophic ranks such as plants [23, 24].

The majority of urban forest studies focused on a single taxonomic group, frequently plants, butterflies, carabids or birds (e.g. [22, 25, 26] and reviews of [27, 28]) or higher taxon or morphospecies levels [29, 30]. So far, few studies have examined the impact of urbanisation on the species diversity and/or functional diversity in forests using a multi-taxa approach. These studies often investigated either taxonomic groups at similar trophic ranks like carabids, rove beetles and spiders [31, 32, 33] or carrion-burying beetles, their phoretic mites, and muscoid flies [34] or focused on species with mutualistic or exploitative relationships [34, 35] or with similar life-history traits [20]. Most multi-taxa urban studies were conducted in openland habitats [19, 29, 35] or over a variety of habitat types [7]. To our knowledge, no studies were conducted in different-sized urban forests and considered species groups with different trophic ranks.

In this study, we examined the impact of degree of urbanisation and forest size on the species and functional diversity of vascular plants and ground surface-active ants and spiders in forest sites in the city of Basel (Switzerland) and its suburban surroundings. The forests examined in our study are very small and embedded in a small-scattered landscape, where settlements and green areas are located within short distances. A rural–urban gradient approach extending over several kilometres is, therefore, not appropriate in our study area. Instead, we used the percentage cover of sealed area in the closer surroundings of the forests as a measure of degree of urbanisation as suggested by others (e.g. [31, 36]).

The taxonomic groups considered in our study vary in trophic rank and thus in the use of resources available in the urban landscape. Ants are intermediate between the other two groups, as many ant species not only consume animal matter but also some plant material such as nectar or elaiosomes attached to seeds. Many species indirectly consume plant sap as excretion from sucking insects. In contrast, spiders are predators. Neither of the two arthropod groups depends on specific plant species as a resource. Hence, their responses to urbanisation can be expected to be independent of that of plants.

In particular, we hypothesize that the diversity of plants, ants, and spiders (species richness, Shannon diversity and evenness and functional diversity) decrease with both increasing degree of urbanisation and decreasing forest size. These effects will be more pronounced for ants and spiders, because of their higher trophic rank, and for forest specialists due to their narrow habitat range. We further expect that small forests show lower species diversity and thus altered functional diversity and harbour lower percentages of forest specialists in highly compared to less urbanised forest areas. In contrast, the diversity in large forest sites should be less negatively affected by degree of urbanisation.

Secondly, we hypothesize that species composition of plants, ants, and spiders will be altered by the degree of urbanisation and forest size. We expect that species composition in highly urbanised areas will be more similar than in less urbanised areas.

Methods

Study area

The study was conducted in the canton Basel-Stadt (comprising the city of Basel and the municipalities Riehen and Bettingen; hereafter referred to as Basel, Fig 1), Switzerland (47° 34'N, 7°36'E, elevation: 245–522 m a.s.l.). The study area covers 37 km^2, consisting of 26.3 km^2 (70.9%) residential area, 4.5 km^2 (12.1%) agricultural land, 4.4 km^2 (11.7%) forest and 1.7 km^2 (4.5%) water bodies (Statistisches Amt Kanton Basel-Stadt: www.statistik-bs.ch). Basel has 196,471 inhabitants and a population density of 5320 inhabitants km^{-2} (www.statistik-bs.ch). Total annual precipitation averages 842 mm and annual mean temperature is 10.5°C (records from 1981 to 2010, www.meteoswiss.admin.ch). Most study sites were state owned and accessible to the public. Some forest was privately owned but managed by the forestry authorities. Permission for fieldwork was obtained from landowners, managers, and the authority responsible for the forests (Amt für Wald beider Basel).

Characteristics of the forests

To investigate the potential effects of degree of urbanisation and forest area on the species diversity of vascular plants, and soil surface-active ants and spiders, we chose 26 deciduous forests, belonging to the *Fagetum* association [37] and ranging in size from 258 m^2 to 50,000 m^2 (Fig 1; S1 Table; S2 Table). The forest sites examined differ in their historical development and consequently in age. Twenty of them are surrounded by settlements and agricultural lands and are no longer connected to large continuous forests (> 40 ha). These forest patches are either remnants of former large continuous forests (fragments) or a result of abandonment of orchards or planted after 1884 (planted; see S1 Table and S2 Table for detailed description of


N
River Rhine
0
1
2
3
4
5 km

Fig 1. Location of the study area in Northwestern Switzerland and the distribution of the forests examined in the area of Basel-Stadt. The investigation area is surrounded by dense settlements in Germany (north), France (northwest) and Switzerland (south-west).

https://doi.org/10.1371/journal.pone.0199245.g001

forests). For each of these twenty forests, we calculated the shape index following Gyenizse et al. [38]. A shape index of 1 corresponds to a circular area, which is considered as most stable and resistant against biotic and abiotic effects from the surrounding landscape [38].

Vegetation survey

In each forest, we installed six sampling plots measuring 4 m × 4 m. Plots had a minimum distance of 1 m to the forest edge or permanent trails to minimize potential edge effects. We assessed species richness of vascular plants in the ground vegetation ($\leq$ 40 cm) and cover of single species in a 2 m × 2 m subplot established in a randomly chosen corner of each 4 m × 4 m plot using the Braun-Blanquet scale [39]. To complete the plant species list in the entire sampling plot, additional species found in the other three 2 m × 2 m subplots were recorded.

Ant and spider sampling

We conducted pitfall trapping to sample ground surface-active ants and spiders. We installed a trapping grid in each of the forests examined. We arranged twelve pitfall traps (plastic cups: 5.8 cm diameter; fluid: 60 ml of water–detergent solution) in two rows with six traps each in a trap-grid system. The distance of the traps between and within the rows was 5 m. The size of the pitfall grid was determined by the smallest fragment, which was thus comprehensively sampled. A dummy of a grid of corresponding size was placed with closed eyes on a map showing forest cover and paths for the larger fragments thus avoiding prior knowledge of vegetation cover or topography when selecting the location for the pitfall trap grids. If necessary the grid was moved to be entirely within the forested area. To account for seasonal differences in activity among species, we operated pitfall traps once in spring, three times consecutively in summer, and once in autumn 2014. Traps were exposed for 7 days before being collected, which resulted in a maximum of 60 trap weeks per forest site (12 traps × 5 sampling weeks).

We transferred trap contents to 70% ethanol for further processing. We identified individuals to the species level following the keys of Seifert [40] and Ward et al. ([41]; *Colobopsis truncata*) for ants and Roberts [42, 43] and Nentwig et al. ([44], <www.araneae.unibe.ch>, version 03.2017) for spiders. In ants, the winged reproductive castes (queens and males) were not considered in the analyses because in contrast to workers it is not clear whether they originated in the study site (123 of 16,465 individuals; 0.75%). We also excluded workers, which were too damaged to allow for species identification (0.13%). Three strictly arboreal species were likewise excluded, as they cannot be recorded in a representative way using pitfall traps. However, arboreal ants, which also have ground surface-activity, were retained [45]. Likewise, we excluded juvenile stages (1211 of 5327 individuals; 22.7%) and adult individuals of spiders, whose identification features (palpal bulbs, epigyne) were missing or destroyed (254 of 5327 individuals; 4.8%), from analyses.

Trait data

We assigned each plant species in one of the following two groups: forest species and non-forest species according to Delarze et al. [46]. For ant species, information on habitat specificity (forest specialist, generalist and open-land species) was designated from Seifert [40] and for spider species from Hänggi et al. ([47]; S3 Table). We called spider species forest specialists when they occur in deciduous forests. Edge species were excluded from this group. For each

Table 1. Species traits of plants, ants, and spiders.

Trait	Type	Description
Plants		
Life form[1]	Categorical	Macrophanerophyte; nanophanerophyte; chamaephyte; hemicryptophyte; geophyte; therophyte
Reproduction type[1]	Categorical	Sexual; mixed
Ecological strategy[1]	Categorical	Following Grime (1979): C; CR; CS; CSR; S; SR
Pollination syndrome[1]	Categorical	Insects; wind
Seed dispersal type[2]	Categorical	Zoochory; anemochory; hemerochory; autochory; hydrochory
Seed mass[1]	Continuous	Mean of seed mass (mg)
Ants		
Body size[3, 4]	Continuous	Maximum of the total length of workers (mm)
Main nest stratum[4]	Categorical	Wood or litter; soil or crevices; both
Number of queens[4]	Categorical	Monogynous; oligogynous; polygynous
Main food type[4]	Categorical	Animal matter; animal matter and carbohydrates; carbohydrates; grains
Spiders		
Body size[5]	Continuous	Mean body size (mm) weighted by the proportion of males and females recorded in this study
Hunting mode[6]	Categorical	Web building; hunting (including active hunting and ambush)

Source

[1] [37]

[2] [38]

[3] species descriptions in the taxonomic literature, sources listed under 4, and own measurements

[4] [29] and three web-based resources (www.antwiki.org, www.ameisenwiki.de, www.antweb.org)

[5] [33]

[6] [39]

https://doi.org/10.1371/journal.pone.0199245.t001

taxonomic group, we selected a set of species traits, which we considered to influence species' response to urbanisation-related factors (Table 1 and S3 Table).

Data of six plant traits (life form, reproduction type, ecological strategy following Grime [48], pollination syndrome, seed dispersal type and seed mass) were obtained from the database BiolFlor [49] and Müller-Schneider [50]. We obtained trait information for ants (body size of workers, main nest stratum, queen number, main food source) from Seifert [40], three web-based resources (<www.antwiki.org>, <www.ameisenwiki.de>, <www.antweb.org>) and in a few cases from own measurements or taxonomic species descriptions (Table 1 and S3 Table). For spider species, we assembled data of body size, and hunting mode from literature [44, 51] (Table 1 and S3 Table).

Environmental characteristics

We estimated total cover of ground vegetation in each of the plots from the vegetation survey using the Braun-Blanquet scale [39]. Canopy closure was assessed based on three photographs in each plot and determined with the pixel counting function of Adobe Photoshop (version 10.0.1).

To examine any potential influences of soil characteristics on plant diversity, three soil samples were collected in each vegetation plot using a metal cylinder (depth: 5 cm; diameter 5.05 cm; volume 100 cm^3) in October 2014. We pooled and mixed the three soil samples of a plot and transported them to the laboratory, where they were sieved (mesh size 2 mm) and dried at 50˚C for 96 h. We determined soil moisture content (%) using the fresh to dry weight ratio and assessed soil pH in distilled water (1:2.5 soil:water) [52]. We determined total soil organic matter content (SOM, %) as loss-on-ignition of oven dried soil at 750˚C for 16 h [52]. We assessed total soil organic nitrogen content (orgN, %) using the standard method of Kjeldahl [53]. Finally, we determined total phosphorus content of soil (orgP, μg PO_4^{3-} g^{-1}) using the molybdenum blue method [54].

We measured biotic and abiotic environmental characteristics in the pitfall trap plots during the autumn pitfall trap survey. To assess the complexity of the vegetation structure and the amount of dead woody debris, we used a slight modification of the point intercept method [55]. In each grid of traps, we installed a transect line in the centre of the two rows. At the beginning of the transect line, we inserted a pin vertically into the ground and recorded the number of times the pin was touched by different plant specimens up to 2 m (hereafter referred to 'vegetation structure') and by dead woody debris on the forest floor (hereafter referred to 'amount of dead wood'). We repeated this procedure at intervals of 1 m resulting in a total of 26 measuring points per forest site.

To assess soil and litter characteristics, we divided the trap-grid system into three sections with each including four traps. In each grid section, we collected four soil samples. We pooled and mixed them to yield a total of three soil samples per trapping grid. In the centre of each grid section, leaf litter was collected in an area measuring 20 cm × 20 cm, dried and weighed. To assess the moisture content and pH of soil and litter and soil organic matter content, we applied the same methods as described above.

Environmental factors were used to characterize the forest sites and to explain the patterns of diversity of the focal groups rather than to examine their own response to urbanisation and forest size. We assessed soil and litter variables, vegetation structure and amount of dead wood in autumn 2014. This is adequate for soil variables because soil pH, SOM, total soil organic nitrogen and total phosphorus content are relatively constant over the whole vegetation period in the forests examined [56]. For leaf litter the autumn sampling captures the year's input. In addition to humidity also temperature can affect biodiversity or arthropod activity. We therefore measured soil temperature close to the surface (0–5 cm) hourly at the edge of the pitfall grid throughout the study period. As the study focused on the ground-surface active ants and spiders, soil surface temperature was considered to be the most appropriate measure for temperature, and air temperature higher up in the vegetation, where some species also forage can be expected to be correlated. However, due to high degrees of vandalism the temperature data were incomplete and could not be used in the models. A finer-scaled soil temperature survey conducted in nine of the forest sites, however, revealed only relatively small differences among the forests [56].

Landscape characteristics and recreational pressure

For each forest, we derived land cover data of six landscape characteristics from satellite images (Google Earth, 2009). Around the most central sampling plot in each forest, we determined the percentage cover of built-up area and traffic infrastructure, urban green space (comprising gardens, parks and allotments), agricultural land and forest cover within radii of 200 m and 500 m using the pixel counting function of Adobe Photoshop (version 10.0.1). The percentage cover of sealed area (built-up area and traffic infrastructure) was used as a measure of the degree of urbanisation. Because the percentage cover of sealed area inter-correlated with the percentage covers of the other three landscape elements (all $P < 0.008$, S4 Table), we did not consider the percentage covers of these landscape elements for data analyses.

We used two different measures to estimate the impact of recreational pressure in the forest sites: (1) path density expressed as the total length of paths and forestry trails per forest site (in m/ha), and (2) the total trampled area within a forest (expressed in percentage of forest area).

Data analyses

Statistical analyses were performed in R ver. 3.0.2 (www.r-project.org) and were carried out separately for the three taxonomic groups at the forest site level. Species richness consists of the total number of species recorded in all vegetation plots and pitfall traps, respectively, over the whole sampling period. In plants, we calculated Shannon diversity and evenness for each of the six vegetation plots separately and averaged them per forest site. In the ant and spider sampling, most of the forest sites were exposed to a variety of disturbances including vandalism, which caused the loss of several traps (72 out of 1560 traps, 4.6%; S5 Table). Therefore, we calculated sample-based rarefied species richness using the *specaccum* function in the package *vegan* in R. Due to positive correlations between observed and sample-based rarefied species richness (both, ants and spiders: $r_s = 1.00$, $n = 26$, $P < 0.001$), we only used rarefied species richness in the subsequent analyses (hereafter referred to as 'species richness'). For ants, where numbers can be inflated when a trap is close to a nest, we used the proportion of traps in which a species was present to calculate Shannon diversity and evenness instead of abundance data. We further used number of individuals per trap (individual density) instead of abundance data to compare Shannon diversity and evenness among forest sites for spiders.

Preliminary analyses revealed correlations between the two radii of degree of urbanisation and the two measures of recreational pressure. In the vegetation plots, SOM further was positively correlated with soil orgN, while there were inter-correlations between soil and litter characteristics in the trap-grid system (soil moisture vs. litter moisture: $r = 0.52$, $n = 26$, $P = 0.006$; soil pH vs. litter pH: $r_s = 0.56$, $n = 26$, $P = 0.003$). Therefore, we only considered degree of urbanisation within the 500-m radius, path density and soil orgN in plants and litter moisture content and litter pH in ants and spiders in the subsequent analyses. Furthermore, the historical development of forests was confounded with forest size (see S4 Table for further details). Forest size thus could not be considered independently from the historical development of the forests.

Based on the percentage cover of sealed area in their surroundings, we classified the forests into areas with low (< 15%), medium (15–30%) or high (> 30%) degrees of urbanisation. We also divided forests into three size classes: small (< 4000 m^2), medium-sized (4000–10,000 m^2) or large (> 10,000 m^2) forests (S2 Table). While these size classes also capture variations in forest history, for simplicity, we refer to these categories as forest size throughout the results section. The three size and three urbanisation classes were based on the distribution of available fragment sizes and percentages of sealed area following [56]. We considered the degree of urbanisation and forest size either as continuous variables (first approach) or as factors (second approach) in the statistical analyses to examine their potential effects on species diversity (species richness, Shannon diversity and evenness). However, because the two approaches revealed very similar results, we only present the results of the second approach.

We applied generalized linear models (GLM) with quasi-Poisson distributed errors using log-link function to examine potential effects of the degree of urbanisation, forest size and the corresponding interaction on species diversity and the percentages of forest specialists, and ANCOVA for the functional dispersion of the three taxonomic groups. We used degree of urbanisation (three classes), forest size (three classes) and shape (three classes: continuous forests (no shape index), shape index 1–1.5, shape index > 1.5) and management of forest sites ('time since last thinning': ≤ 3 years, 4–10 years or > 10 years ago) as factors, and path density and canopy closure as cofactors in the GLM and ANCOVA models of all three taxonomic groups. In plants, we further included soil moisture content, soil pH, soil orgN and orgP and cover of ground vegetation as cofactors in the GLM and ANCOVA models (S2 Table). For ants and spiders, we used SOM, litter moisture content and litter pH, amount of litter biomass, vegetation structure and amount of dead wood as cofactors in the GLM and ANCOVA models (S2 Table). In ants and spiders, we further tested the impact of these factors on the percentages of generalist species. All the environmental factors listed above were included into models as covariables. The models were then reduced following a stepwise procedure, which resulted in the dropping of several covariables. We performed multiple comparisons (Tukey contrasts) to compare differences among degrees of urbanisation, forest size, forest shape and time since last thinning, respectively, using the *glht* function in the *multcomp* package in R [57].

To show whether degree of urbanisation affected species composition of plants, ants and spiders, we used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measures. Data were square-root-transformed and Wisconsin double standardization was applied. This type of transformation involves standardization of species maxima, followed by relativization of sample total [58] Species, which were recorded in only one site, were excluded from the analyses.

Permutational multivariate analyses of variance (PERMANOVA) were used to test whether degree of urbanisation, forest size and local forest characteristics affected species composition of plants, ants and spiders [59]. The local forest characteristics were included as cofactors (S6 Table). For plants, soil moisture, soil pH, total soil phosphorous content, total soil nitrogen content, and ground vegetation cover were thus included in the analysis. For ants and spiders, path density, canopy closure, total soil organic matter content, litter moisture, litter pH, litter biomass, amount of dead wood, and vegetation structure were included as cofactors. For all three groups of organisms, we further included the shape index and the time since last thinning as factors. All PERMANOVA tests were based on 999 permutations of the untransformed raw data, using the *adonis* function in the vegan R-package [60].

As a measure for functional diversity we calculated functional dispersion for each taxonomic group according to Villéger et al. [61] using the *dbFD* function with Cailliez corrected distance matrices in the package *FD* in R [62]. As for the NMDS and PERMANOVA analyses, we only used those species that occurred in more than one forest site. We used ANCOVA to examine the impact of degree of urbanisation, forest size and local forest characteristics on the functional dispersion of plants, ants, and spiders.

Results

Across the 26 forests, we recorded a total of 130 vascular plant species (30.7 species per forest, range: 17–53 species; S5 Table). Eighty-three of the 130 plant species (63.8%) were forest specialists. The most common plant species in the ground vegetation layer were *Hedera helix* and *Quercus robur*, which occurred in 26 forests and *Fraxinus excelsior* and *Geum urbanum*, which were found in 25 forests.

Overall, we collected 16,321 ants belonging to 28 species in the 26 forests examined. On average, we captured 10.0 ant species (range: 6–16 species) per forest (S5 Table). Among ant species, 10 were forest specialists or dependent on wood for their nest construction (35.7% of species found), while the reminder were habitat generalists (5 species; 17.9%) or even open-land species (13 species; 46.4%). *Myrmica rubra*, a generalist species, which is often found in urban habitats, comprised 41.7% of all ants collected. It occurred in 19 of the 26 sites, with 75.3% of individuals collected in a particular site. Six ant species were more widespread: *Myrmecina graminicola* and *Temnothorax nylanderi* (26 forests each), *Lasius niger* and *Stenamma debile* (23 each), *Lasius brunneus* (22) and *Myrmica ruginodis* (20).

We collected 5,327 spiders belonging to 109 species. On average, 18.3 spider species (range: 10–31 species) were captured per forest (S5 Table). In spiders, 30 species were forest specialists (27.5%), 57 habitat generalists (52.3%) and 21 open-land species (19.3%). The most common spider species were *Tenuiphantes flavipes* (26 forests), *Trochosa terricola* (21), *Diplostyla concolor* and *Pardosa saltans* (19 each).

Effects of degree of urbanisation on species diversity

Plant species richness, the percentage of forest specialists and Shannon diversity of plants were affected by the degree of urbanisation (Table 2; Fig 2). While the species richness and Shannon diversity of plants decreased with increasing degree of urbanisation (Fig 2A and 2C), the percentage of forest specialists was slightly higher in forests located in areas with either a low or high degree of urbanisation compared to forests situated in areas with a medium degree of urbanisation (Fig 2B). Furthermore, Shannon evenness of plants tended to decrease in forests with increasing percentage cover of sealed areas in their surroundings (Fig 2D).

In ants, the percentage of generalists was influenced by the degree of urbanisation, being slightly higher in forests with dense settlements in their surroundings than in forests located in areas with low or medium degrees of urbanisation (Table 3). In contrast, species richness, Shannon diversity and evenness of ants were not affected by the degree of urbanisation (Table 3).

In spiders, both the percentages of forest specialists and generalists were influenced by the degree of urbanisation (Table 4). The percentage of forest specialists was lower in forests situated in areas with medium degree of urbanisation than in forests located in areas with high or low degree of urbanisation. In contrasts, the percentage of generalists was higher in forests located in areas with medium and high degrees of urbanisation than in forests surrounded by sparse settlements. However, the species richness, Shannon diversity and evenness of spiders did not differ among the urbanisation classes. We found an interaction between degree of urbanisation and forest size for the Shannon evenness of spiders: Small forests located in areas with a low degree of urbanisation had lower Shannon evenness indices than small forests

Table 2. Summary of GLM analyses examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil characteristics (moisture, pH, soil orgN and orgP) and cover of ground vegetation on the species richness, percentage of forest specialists, Shannon diversity and evenness of vascular plants.

	Species richness[1]			Percentage of forest specialists			Shannon diversity			Shannon evenness		
	df	F	P	df	F	P	df	F	P	df	F	P
Degree of urbanisation	2,23	8.43	**0.004**	2,23	4.59	**0.029**	2,23	7.71	**0.004**	2,23	3.44	0.056
Forest size	2,21	0.04	0.96	2,21	2.07	0.16	2,21	1.78	0.20	2,21	4.88	**0.021**
Shape index	2,19	1.43	0.27	2,19	18.59	**<0.001**	–	–	–	–	–	–
Time since last thinning	–	–	–	2,17	1.47	0.26	2,19	2.64	0.10	2,19	5.57	**0.014**
Path density	–	–	–	–	–	–	–	–	–	–	–	–
Canopy closure	1,18	7.84	**0.015**	1,16	9.53	**0.008**	–	–	–	–	–	–
Soil moisture content	–	–	–	1,15	2.91	0.11	1,18	7.83	**0.012**	1,18	9.85	**0.006**
Soil pH	–	–	–	1,14	2.63	0.13	–	–	–	–	–	–
Soil orgN[1]	–	–	–	–	–	–	1,17	1.23	0.28	1,17	1.50	0.24
Soil orgP[1]	1,17	3.47	0.085	–	–	–	–	–	–	–	–	–
Cover of ground vegetation	–	–	–	–	–	–	†	†	†	†	†	†
Degree of urbanisation*forest size	4,13	1.41	0.28	–	–	–	–	–	–	–	–	–

Significant P-values (< 0.05) are in bold

[1] log-transformed

–Factor was excluded from the model by step-wise reduction

† Factor was not included in the model

https://doi.org/10.1371/journal.pone.0199245.t002

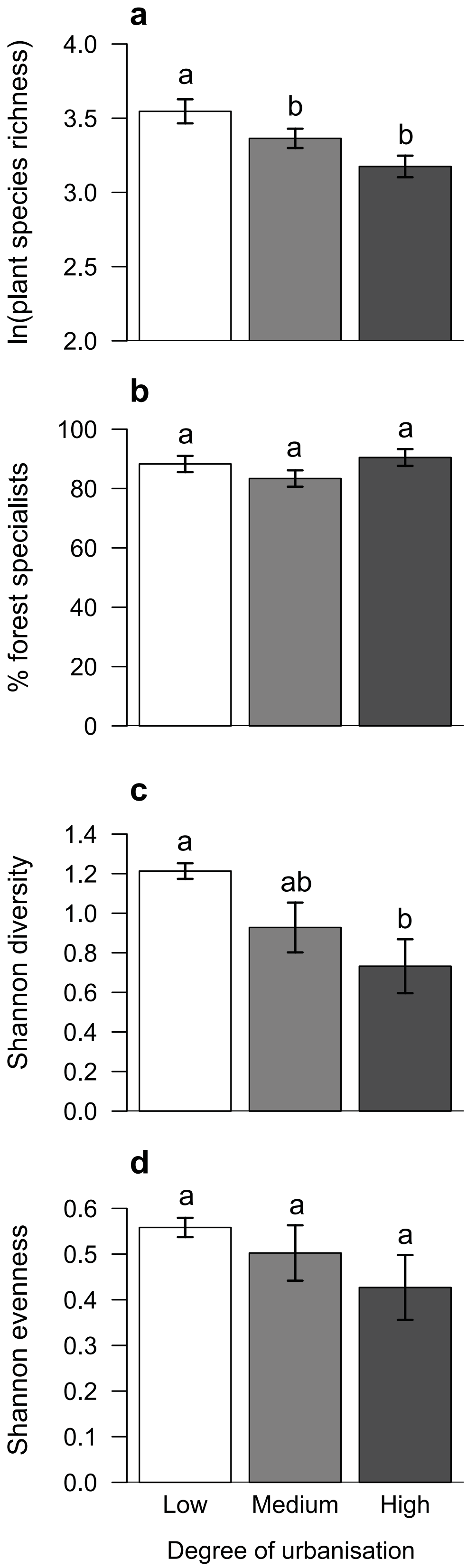

a
ln(plant species richness)
4.0
3.5
3.0
2.5
2.0
a
b
b
b
% forest specialists
100
80
60
40
20
0
a
a
a
c
Shannon diversity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
ab
b
d
Shannon evenness
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
a
a
Low
Medium
High
Degree of urbanisation

Fig 2. Plant species richness (a; mean ± SE), percentage of forest specialists (b), Shannon diversity (c) and evenness (d) in forests, which were located in areas with different degrees of urbanisation.

https://doi.org/10.1371/journal.pone.0199245.g002

located in areas with medium and high degrees of urbanisation, whereas medium-sized and large forests showed similar Shannon evenness indices in areas with different degrees of urbanisation.

Effects of the size and shape of forests on species diversity

Shannon evenness of plants slightly increased with forest size, but was not affected by the shape of the forests (Table 2). In contrast, the percentage of forest specialists was influenced by the shape of forests (Table 2; S1 Fig), but did not differ among size classes (Table 2). A higher percentage of forest specialists was found in large continuous forests and forests with a shape index between 1.0 and 1.5 than in forests with a shape index higher than 1.5 (S1 Fig). The species richness and Shannon diversity of plants were neither influenced by the size nor shape of forests (Table 2).

In ants, the percentage of forest specialists and Shannon diversity of ants were positively related to forest size (Table 3; S1 Fig), but were not influenced by the shape of forests. The species richness of ants and percentage of generalists of ants were neither influenced by the size nor the shape of forests (Table 3).

Similar to ants, the percentage of spider forest specialists was higher in large than in medium-sized and small forests (Table 4; S1 Fig), but was not influenced by forest shape. Shannon evenness tended to be affected by forest size, being slightly higher in medium-sized than in small forests. Furthermore, Shannon evenness tended to be influenced by the shape index of forests. Large continuous forests and forests with a shape index between 1.0 and 1.5 exhibited

Table 3. Summary of GLM analyses examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil organic matter content, litter characteristics (moisture, pH) and structural diversity measures (litter biomass, vegetation structure and amount of dead wood) on the species richness, percentages of forest specialists and generalists, Shannon diversity and evenness of ants.

	Sample-based rarefied species richness			**Percentage of forest specialists**			**Percentage of habitat generalists**			**Shannon diversity**			**Shannon evenness**		
	df	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**	**Df**	**F**	**P**
Degree of urbanisation	2,23	2.94	0.083	2,23	1.84	0.21	2,23	4.31	**0.049**	2,23	3.21	0.06	2,23	0.33	0.72
Forest size	2,21	2.71	0.10	2,21	6.09	**0.018**	2,21	0.71	0.51	2,21	4.71	**0.023**	2,21	1.57	0.15
Shape index	–	–	–	2,19	1.20	0.34	2,19	2.56	0.14	–	–	–	–	–	–
Time since last thinning	–	–	–	2,17	1.83	0.21	2,17	2.59	0.13	–	–	–	–	–	–
Path density	1,20	6.68	**0.022**	–	–	–	–	–	–	1,20	7.45	**0.014**	–	–	–
Canopy closure	–	–	–	1,16	5.29	**0.044**	–	–	–	–	–	–	1,20	1.57	0.23
Soil organic matter content^1	–	–	–	–	–	–	1,16	5.79	0.**040**	–	–	–	–	–	–
Litter moisture content	–	–	–	1,15	2.46	0.15	1,15	6.31	0.**033**	–	–	–	–	–	–
Litter pH	1,19	7.12	**0.018**	–	–	–	–	–	–	1,19	5.38	**0.032**	–	–	–
Amount of litter biomass^1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vegetation structure^1	–	–	–	1,14	1.58	0.24	1,14	5.65	**0.041**	–	–	–	–	–	–
Amount of dead wood	1,18	1.36	0.13	–	–	–	1,13	1.61	0.24	1,18	6.47	0.**020**	–	–	–
Degree of urbanisation*forest size	4,14	1.09	0.40	4,10	2.55	0.10	4,9	1.93	0.19	–	–	–	–	–	–

Significant P-values (< 0.05) are in bold

^{1} log-transformed

–Factor/Co-factor was excluded due to by step-wise model reduction procedure

https://doi.org/10.1371/journal.pone.0199245.t003

Table 4. Summary of GLM analyses examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil organic matter content, litter characteristics (moisture, pH) and structural diversity measures (litter biomass, vegetation structure and amount of dead wood) on the species richness, percentages of forest specialists and generalists, Shannon diversity and evenness of spiders.

	Sample-based rarefied species richness			Percentage of forest specialists			Percentage of habitat generalists			Shannon diversity			Shannon evenness		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Degree of urbanisation	2,23	0.60	0.56	2,23	9.30	**0.002**	2,23	4.48	**0.028**	2,23	1.36	0.30	2,23	1.67	0.23
Forest size	2,21	0.02	0.98	2,21	3.96	**0.039**	2,21	0.29	0.75	2,21	1.90	0.20	2,21	3.77	0.051
Shape index	–	–	–	–	–	–	–	–	–	2,19	1.33	0.31	2,19	3.38	0.066
Time since last thinning	–	–	–	–	–	–	–	–	–	2,17	1.57	0.26	–	–	–
Path density	–	–	–	1,20	2.54	0.13	1,20	4.36	0.053	–	–	–	1,18	1.94	0.19
Canopy closure	1,20	4.33	0.052	–	–	–	–	–	–	1,16	1.88	0.20	–	–	–
Soil organic matter content[1]	–	–	–	1,19	2.67	0.12	1,19	1.78	0.20	–	–	–	–	–	–
Litter moisture content	1,19	5.29	**0.034**	–	–	–	–	–	–	1,15	2.17	0.17	–	–	–
Litter pH	1,18	1.23	0.28	1,18	7.20	**0.016**	1,18	2.64	0.12	–	–	–	–	–	–
Amount of litter biomass[1]	–	–	–	1,17	4.41	0.051	1,17	1.77	0.20	–	–	–	–	–	–
Vegetation structure[1]	–	–	–	–	–	–	1,16	3.68	0.073	1,14	2.06	0.18	1,17	1.77	0.21
Amount of dead wood	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Degree of urbanisation*forest size	–	–	–	–	–	–	–	–	–	4,10	1.51	0.27	4,13	5.20	**0.010**

Significant P-values (< 0.05) are in bold

[1] log-transformed

–Factor was excluded from the model by step-wise reduction

https://doi.org/10.1371/journal.pone.0199245.t004

a more even spider species distribution than forests with a shape index larger than 1.5. However, species richness, percentage of generalists and Shannon diversity of spiders were neither affected by the size nor shape of the forests (Table 4).

Effects of forest site characteristics on species diversity measures

Plant species richness decreased with increasing canopy closure of forests ($r_s = -0.61$, n = 26, $P < 0.001$), while the percentage of forest specialists increased ($r_s = 0.47$, n = 26, P = 0.017; Table 2). Both Shannon diversity and evenness of plants were positively related to soil moisture content (diversity: $r_s = 0.52$, n = 26, P = 0.007; evenness: r = 0.42, n = 26, P = 0.031). Furthermore, Shannon evenness of plants was affected by the time since last thinning (Table 2). It was higher in forests, which were managed recently (≤ 3 years or 4–10 years) than in forests, which were thinned last time more than 10 years ago. However, path density, soil pH, soil orgN and orgP and the cover of ground vegetation did not influence any of the plant diversity measures examined (Table 2).

In ants, species richness was negatively affected by litter pH ($r_s = -0.53$, n = 26, P = 0.005) and tended to increase with path density (r = 0.38, n = 26, P = 0.058; Table 3). The percentage of forest specialists was influenced by canopy closure, being highest at moderate structural diversity of vegetation. The percentage of generalist ant species was positively affected by soil organic matter, litter pH, and vegetation structure (Table 3). However, the Spearman correlations for these covariables were not significant (all $P > 0.2$). Shannon diversity of ants tended to be positively affected by path density ($r_s = 0.37$, n = 26, P = 0.062), and negatively by litter pH ($r_s = -0.35$, n = 26, P = 0.077) and amount of dead wood (Table 3). However, the Spearman correlation for the latter was not significant. Shannon evenness of ants was not affected by any of the forest characteristics.

The species richness of spiders decreased with litter moisture content (r = –0.41, n = 26, P = 0.038) and tended to be affected by canopy closure (Table 4). However, the latter was not a linear relationship. The percentage of forest specialists was influenced by litter pH with species richness highest at intermediate values of pH (Table 4). However, none of the forest characteristics examined had a significant impact on the percentage of generalist species, and Shannon diversity and evenness of spiders (Table 4).

Species composition

For plants, multivariate analysis using NMDS showed that plant species composition shifted from low to high degrees of urbanisation but with some overlap (Fig 3A). PERMANOVA confirmed that plant species composition was significantly affected by forest size ($F_{2,19} = 2.42$, $P = 0.005$). However, only a marginal tendency was found for degree of urbanisation ($F_{2,19} = 1.47$, $P = 0.099$). Plant species composition was also significantly affected by soil moisture ($F_{1,19} = 2.82$, $P = 0.014$) and total soil organic nitrogen content ($F_{1,19} = 3.59$, $P = 0.001$). Some common species showed marked differences in their frequencies depending on the degree of urbanisation or forest size (S7 Table). For example, the frequency of *Arum maculatum* and *Duchesnea indica* decreased with increasing degrees of urbanisation, while *Alliaria petiolata* was most frequent at intermediate degrees of urbanisation, and *Tilia platyphyllos* was most frequent in sites with high degrees of urbanisation.

Similar to the findings for plant species composition, ant species composition showed a shift from areas with a low degree of urbanisation to those with a high degree of urbanisation, though with some overlap (Fig 3B). Moreover, PERMANOVA showed that ant species composition was significantly affected by the degree of urbanisation ($F_{2,15} = 1.86$, $P = 0.045$). Ant species composition was also affected by forest size ($F_{2,15} = 2.79$, $P = 0.005$). Furthermore, canopy cover was also significantly affecting ant species composition ($F_{2,15} = 2.30$, $P = 0.035$). While many common species were similarly often present in sites with different degrees of urbanisation or of different size, some showed marked differences (S7 Table). For example, the generalist species *Myrmica rubra* occurred in all sites with high degrees of urbanisation, but only in three quarters of sites with a medium degree of urbanisation, and in just over half of sites with a low degree of urbanisation.

Similarly, for spiders, there was a shift in species composition from highly to less urbanised areas ($F_{2,17} = 2.63$, $P = 0.001$; Fig 3C). Spider species composition was also affected by forest size ($F_{2,17} = 1.62$, $P = 0.032$). Furthermore, spider species composition was influenced by most forest characteristics examined: litter moisture content ($F_{1,17} = 1.86$, $P = 0.028$), SOM ($F_{1,17} = 1.73$, $P = 0.049$), vegetation structure ($F_{1,17} = 1.72$, $P = 0.047$), amount of dead wood ($F_{1,17} = 1.98$, $P = 0.015$). As for plants and ants, some spider species showed marked differences in their frequency of occurrence in forests with different degrees of urbanisation and of different size (S7 Table). Examples include *Histopona torpida* and *Palliduphantes pallidus*, which decreased in frequency with increasing degrees of urbanization, and *Diplostyla concolor*, which was most frequent in highly urbanized sites.

Functional dispersion

Plant functional dispersion was affected by the degree of urbanisation ($F_{2,16} = 3.92$, $P = 0.041$) and forest size ($F_{2,16} = 3.68$, $P = 0.049$; S8 Table). Furthermore, plant functional dispersion was influenced by the time since last thinning (S8 Table).

Considering ants, functional dispersion tended to be influenced by forest size ($F_{2,13} = 3.68$, $P = 0.054$) (S9 Table). Furthermore, ant functional dispersion was significantly affected by litter moisture ($F_{2,13} = 12.63$, $P = 0.004$; S9 Table). In contrast spider functional dispersion was not significantly influenced by degree of urbanisation, forest size, or habitat characteristics (S9 Table).

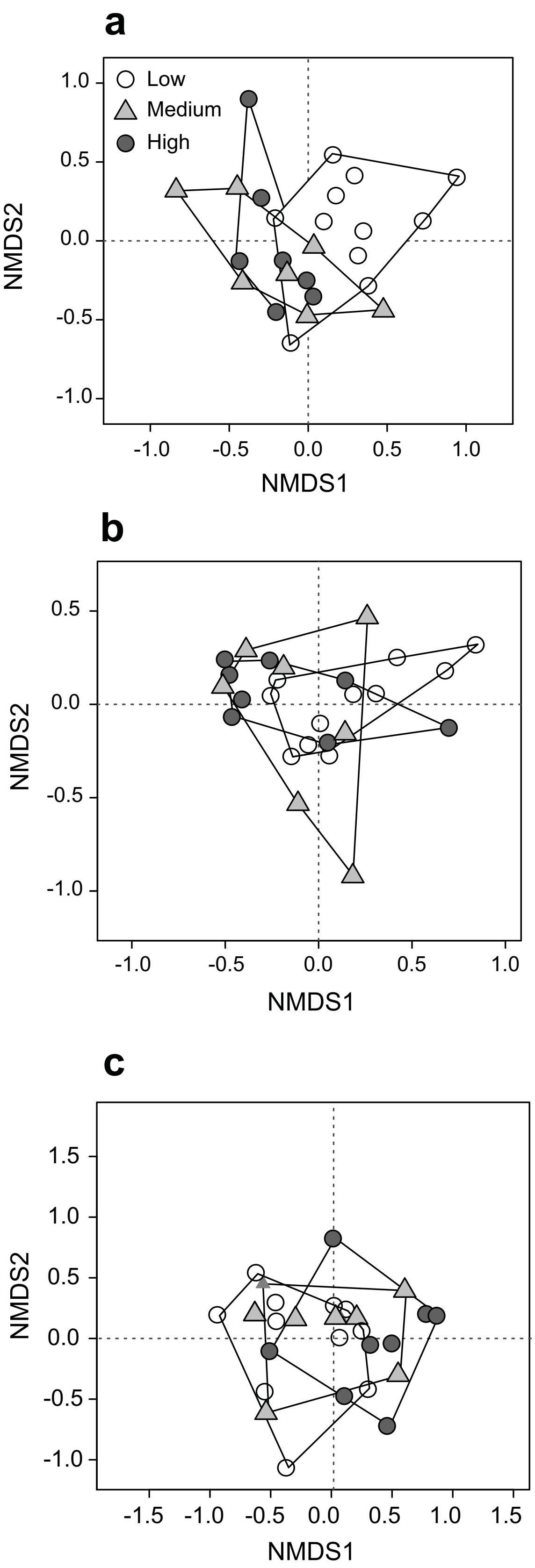

a
○ Low
△ Medium
● High
NMDS2
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
NMDS1
b
NMDS2
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
NMDS1
c
NMDS2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS1

Fig 3. NMDS of (a) plant, (b) ant and (c) spider species composition. Forests sites are grouped according to their degree of urbanisation (low, medium, high).

https://doi.org/10.1371/journal.pone.0199245.g003

Discussion

Our results showed that the response to the degree of urbanisation and forest size considerably varied among the three taxonomic groups. However, when we grouped species according to their habitat specificity, we observed a reduction in the percentage of forest specialist species with decreasing forest size in both arthropod groups. In addition to degree of urbanisation and forest size, species diversity and species composition of plants were determined by abiotic site characteristics and those of ants and spiders by the structural diversity of both leaf litter and vegetation.

Effect of urbanisation on species diversity

During the last decades, the worldwide urban sprawl and the subsequent destruction and isolation of green areas represent major drivers for local species extinction [3]. Hence, we expected a decrease in species diversity (species richness, Shannon diversity and evenness) with increasing degree of urbanisation. However, we only found this to be the case in plants. Cameron et al. [63] reported similar results for plant species richness, but did not find any effect on plant diversity. In contrast, McKinney [28] found the highest number of plant species in areas with medium degree of urbanisation, whereas Vallet et al. [25] did not detect any difference in total species richness of plants between urban and rural woodlands. These outcomes may be due to differences in the number of non-native plant species, the spatial dimension of the study areas and the degree of urbanisation associated with differences in habitat diversity ([28] and references therein). In our study sites we only found very few neophytes.

In ground surface-active ants and spiders, the lack of response of species diversity to urbanisation contrasted our hypothesis and the findings of other studies conducted on soil arthropods in forests, which showed either a negative (carabids: [16]), hump-shaped (spiders: [32], carabids: [64]) or positive response (spiders: [65, 66]) on species richness in relation to the degree of urbanisation. However, similar results as in our study were reported by Alaruikka et al. [64], who argued that spiders might be more affected by local site characteristics (e.g. structural diversity) than by characteristics at the landscape scale.

The higher sensitivity of plant species richness to degree of urbanisation compared to those of higher trophic rank ants and spiders did not confirm our hypothesis and contrasted findings of several multi-taxa studies (e.g. [28, 35, 67]). Comparisons with these studies, however, should be made with caution, as most of them were conducted in different habitat types and/or considered other taxonomic groups [16, 20, 35]. The taxonomic groups considered in those studies are also often closely related by showing specialised plant-herbivore interactions (e.g. [35]). Contrary to this, the majority of ant and spider species recorded in our study were food generalists and thus may better cope with the loss of some species at lower trophic rank compared to specialised herbivores or predators [23, 68], as long as primary productivity as a whole was sufficient. Another explanation for the observed pattern might be differences in mobility of the three focal groups. As plants are sessile, they are more strongly influenced by their immediate surroundings and can hardly evade unfavourable environmental conditions caused by urbanisation compared to ants and spiders. Furthermore, the seeds of most plant species recorded in the present study are dispersed by animals. Hence, negative impacts of urban sprawl on the behaviour, mobility and diversity of these seed dispersers, may have enhanced the vulnerability of plants to urbanisation.

Several urban studies reported a replacement of forest specialists by generalist species with increasing degree of urbanisation suggesting that forest specialists are more sensitive to urbanisation-related disturbances [31, 32, 65]. While this was the case in ants, plants and spiders showed the lowest percentages of habitat specialists in forests located in areas with medium degree of urbanisation (15–30% sealed area). This finding was unexpected and may be a result of combined effects of differences in habitat diversity in the surroundings, which may be highest at medium levels of urbanisation, and of refugia effects of forests in highly urbanised areas.

Effects of forest size and shape on species diversity

As a consequence of proceeding urban development, many forest sites are characterised by intense isolation and small size. Thus, it is important to examine how habitat size affects biodiversity, and how this factor interacts with the degree of urbanisation in its surroundings. Theory of island biogeography predicts that small habitat patches contain less species than large habitat patches [69]. In this study, however, we did not find a species–area relationship for any of the three taxonomic groups examined. This result rejects our hypothesis and contrasts findings of previous studies on plants [70, 71] and web spiders [72] conducted in urban forests. Partly in line with our finding, Gibb and Hochuli [21] did not record a species–area relationship in spiders either and even reported an increase of ant species richness with decreasing forest size. Most studies, however, which failed to uncover area-related effects on species richness, were typically conducted in forests much larger (e.g. [21]: 4–80 km^2) than those in our study.

Even though forest size did not influence total species richness, we recorded higher percentages of forest specialists of ants and spiders in large than in small and medium-sized forests. Possible explanations might be a higher proportion of edge to different habitat types in small compared to large forests and, thus, a replacement of forest specialists by generalists and open-land species [21, 73]. Indeed, we found higher percentages of open-land species in small than large forests (ants: 32.3% vs. 20.1%; spiders: 11.0% vs. 4.9%). Regarding spiders, most open-land species were hunters in this study. We suggest that they may have temporarily visited forests for foraging rather than permanently living in them. Similarly, foraging ant workers from nests outside the fragments may have visited the edge zone of small forests.

As forest size was not independent of forest history in our study, some of the observed differences in percentage forest specialists for ants and spiders may also be the result of some of the forest sites having previously been non-forested habitats. However, none of the forests were very recent in origin (all the study sites were marked as forest on old maps for at least 44–137 years), and even small fragments harboured forest specialist species. Indeed small forests were not per se less suitable habitats for forest specialists as demonstrated in plants. In our study, interestingly, the shape rather than the size/history of forests was the main predictor of the percentage of forest specialists. Forest sites, which were part of a continuous forests, and forests with a rather circular area (shape index 1–1.5) exhibited a higher percentage of forest specialists than forests with a more complex shape (shape index > 1.5). Hence, even small urban forest sites of comparably recent origin can serve as habitat for numerous forest specialists, if the proportion of edge to other habitat types and associated changes in the abiotic environment are minimized. However, most of the small forest sites in our study were dominated by a few plant species–independent of the degree of urbanisation in their surroundings.

Effects of forest site characteristics on species diversity

Plant species richness and the percentage of forest specialists were related to canopy closure considered as a proxy for light conditions, while soil moisture content was a key predictor of

Shannon diversity and evenness, highlighting the importance of abiotic site characteristics for plant diversity.

Similarly, in ants, canopy closure was important in explaining the percentage of forest specialists. Furthermore, leaf litter characteristics (litter moisture, litter pH) were important determinants for ant diversity. In urban forests, leaf litter biomass can be reduced as a result of recreational use. This would not only affect ant species with nests within this layer, but also the many species foraging there.

In our study, the majority of both spider species and individuals belonged either to the family Linyphiidae (44.0% and 57.9%), which build their webs in leaf litter and mainly low vegetation, or Lycosidae (9.2% and 22.1%), which are active hunters. Hence, we expected a strong response of spiders to changes in the structural diversity of leaf litter and vegetation. Surprisingly, these two variables had no significant role in explaining variation in overall spider diversity. This lack of response may be partly explained by the habitat specificity of spider species, since we observed a trend towards an increase in the percentage of forest specialists with the amount of leaf litter biomass. This positive relationship may be also the reason for the high percentage of forest specialists recorded in large forests, which exhibited a higher amount of leaf litter biomass (mean: 335.2 g m^{-2}) than small and medium-sized forests in this study (157.6 and 138.5 g m^{-2}).

Species composition

Species composition may change even when species richness is maintained [19]. Urban communities can be a subset of the regional species pool, often biased towards generalists, which are better adjusted to a stressful environment [31, 32], or they may be novel by comprising many non-native species [3]. While we recorded few non-native species, the urban forests in this study harboured many generalist and open-land species, in line with other studies (e.g. [31, 32]). This is likely a consequence of differences in disturbance intensity and a small-scale habitat mosaic. Nevertheless, many forest specialists persisted including a few species listed as threatened for Switzerland. However, the red list for ants is out-dated and no such list exists for spiders, and we thus did not analyse threatened species separately. As our fragments were small compared to other studies on this topic (e.g. [21, 31, 71]), our findings highlight the sometimes-overlooked conservation value of even small, heavily disturbed habitats.

PERMANOVA showed that as hypothesized, groups at higher trophic rank were more strongly affected by urbanisation. While this was not the case for species richness and diversity, the shift was visible in species composition. Plant species composition did only show a weak trend towards differences among the urbanisation classes, while species composition of the predaceous spiders significantly shifted with increasing degree of urbanisation. In line with our expectation, spider species composition was more similar in highly than in less urbanised areas. Ants fell between, with highly urbanised areas having a significantly changed species composition. Most spider species are generalist predators. We expected that urbanisation might affect specialised predators or parasites in our study area even more [23]. Indeed, none of the three social parasitic ant species, which use host species to found new colonies, were present in highly urbanised forest sites, even though one was common in seven other sites. Species at high trophic rank, therefore, should receive special attention when managing urban habitats.

Interestingly, forest size was important for explaining species composition of all groups. This may have also partly reflected the effects of the history of the forest sites, as species composition may have not reached equilibrium yet in sites that had been previously non-forested habitats, or in forest fragments whose area has been reduced. This may also have affected some local environmental conditions such as soil-related factors, alongside current effects such as disturbance and forest management. However, none of the forests were very recent in origin. Local abiotic factors (soil moisture and soil orgN) were important drivers for plants species composition. In contrast, only canopy closure helped to explain ant species composition, while spider species composition was affected by both abiotic and structural forest characteristics. These results mirror the importance of local abiotic habitat characteristics as key drivers for plant species diversity measures. Combining results for species composition and diversity we find that both abiotic and structural forest characteristics are important in explaining arthropod diversity and species composition. Structural forest characteristics may be a surrogate for food availability. However, we did not directly measure food availability for arthropods, though e.g. SOM may be related to it, as it supports detrivores and thus potential prey [74, 75]. This finding indicates opportunities to increase the conservation values of urban forests, because local site characteristics are more amenable to management efforts than landscape factors.

Functional dispersion

It is expected that functional dispersion should decrease with increasing urbanisation because of an enhanced influence of environmental filtering in stressful urban environments. Some species fulfil unique roles, while others have similar functions within an ecosystem. Thus, local species loss or shifts in relative abundance can reduce the abundance and efficiency of functional traits in niche space and subsequently ecosystem functioning [76]. The observed changes in species composition in our study should thus translate to changes in functional diversity [61]. Indeed we observed that functional dispersion of plants decreased with increasing degrees of urbanisation. That this decrease in functional dispersion was a result of an increasingly stressful environment, was also supported by the finding that functional dispersion decreased with forest size. Small fragments with a high proportion of edge habitat were assumed to be exposed to most stress.

In contrast to the situation found for plants, functional dispersion in the two arthropod groups was not influenced by these two main factors, with only that of ants showing a non-significant trend to be affected by forest size. Neither did functional dispersion change depending on most of the local environmental factors examined. Given the results from the PERMANOVAs, we would have expected the observed shifts in species composition to result in larger effects on functional dispersion also for the ground surface-active arthropod community. For example, the litter layers in some urban forest fragments were reduced as a consequence of the high levels of disturbance, which could have been expected to reduce habitat quality and thus the presence of functional groups associated with leaf litter.

Conclusions

Our results showed that species richness of the taxonomic groups was not an ideal indicator of biodiversity change in urban landscapes, as it masked shifts in species composition and relative abundance of species with different habitat specificity. Using a multi-taxa approach, we further found that the effect of urbanisation on species composition increased with trophic rank. This highlights the necessity to consider different taxonomic and functional groups in urban planning to maximize conservation value of urban green areas. In the short term, urban planners could focus on small-scale environmental factors, which proved to be important determinants of species diversity and species composition. For example, protection of litter layers and ground vegetation could be enhanced using simple management practices. However, the influence of large-scale factors like the proportion of sealed area in the surroundings and forest size on forest specialists indicates that also more complex changes at the landscape level are essential to maintain vulnerable elements of forest communities.

Supporting information

S1 Fig. Forest specialists in relation to size and shape of urban forests. Percentage forest specialist species of a) ants and b) spiders in fragments of different size; size classes are small (< 4000 m^2), medium-sized (4000–10,000 m^2) and large ($> 10,000$ m^2); and c) percentage of forest specialist species of plants depending on the shape of the fragment. The shape index was calculated following Gyenizse et al. [28]. A shape index of 1 corresponds to a circular area, which is considered as most stable and resistant against biotic and abiotic effects from the surrounding landscape. Classes are A: continuous forest, B: shape index between 1 and 1.5, C: shape index > 1.5.
(DOCX)

S1 Table. Description of forest sites. Characteristics of the 26 forests examined in Basel (Switzerland) and its surroundings.
(DOCX)

S2 Table. Landscape, forest and plot characteristics recorded during field surveys.
(XLS)

S3 Table. Species and trait lists. Species list of (a) vascular plants, (b) ants and (c) spiders. Habitat specificity, conservation status (Red List) and a set of traits, which we considered to influence species' response to urbanisation-related factors are shown. Traits not used for analyses are in parentheses.
(DOCX)

S4 Table. Correlations within and among landscape and site characteristics. Results of Pearson's (r) and Spearman's rank (r_s) correlation, Contingency table (χ^2-test) and Kruskal-Wallis test examining the relationship between observed species richness and rarefied species richness (a) and among landscape and forest characteristics for all three taxonomic groups (b), in the vegetation plots (c) and in the trap-grid system (d)
(DOCX)

S5 Table. Species–site matrices for plants, ants, and spiders. For the arthropod survey, the number of recollected traps per forest site is presented.
(XLSX)

S6 Table. Data used to perform PERMANOVA.
(XLSX)

S7 Table. Percentage of sites in which common species occur for different degrees of urbanisation and forest size classes. Common species are defined as occurring in at least 10 of the sites. Means are given for less common species.
(XLS)

S8 Table. Functional dispersion: Summary of ANCOVAs of plants. Summary of ANCOVAs examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil characteristics (moisture, pH, soil organic nitrogen (orgN) and phosphorus (orgP) content) and cover of ground vegetation on functional dispersion of vascular plants.
(DOCX)

S9 Table. Functional dispersion: Summary of ANCOVAs of ants and spiders. Summary of ANCOVAs examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil organic matter content, litter characteristics (moisture, pH) and structural diversity measures (litter biomass, vegetation structure and amount of dead wood) on functional dispersion of ants and spiders.
(DOCX)

Acknowledgments

We thank A. Hänggi for help with spider identification and R. Neumeyer and B. Seifert for verifications of some ant identifications. We further thank D. Binggeli, J. Hart, D. Milner, K. Reinacher and R. Schneider for sorting of pitfall-trap content. We also thank the foresters (Amt für Wald beider Basel), Christoph Merian Stiftung, Industrielle Werke Basel, Stadtgärtnerei Basel and private owners for access to the study sites. We thank P. Heneberg and three anonymous reviewers for comments on an earlier draft of this manuscript.

Author Contributions

Conceptualization: Ramona Laila Melliger, Brigitte Braschler, Hans-Peter Rusterholz, Bruno Baur.

Data curation: Ramona Laila Melliger, Brigitte Braschler.

Formal analysis: Ramona Laila Melliger, Brigitte Braschler, Hans-Peter Rusterholz.

Funding acquisition: Brigitte Braschler, Bruno Baur.

Investigation: Ramona Laila Melliger, Brigitte Braschler.

Methodology: Ramona Laila Melliger, Brigitte Braschler, Hans-Peter Rusterholz, Bruno Baur.

Supervision: Hans-Peter Rusterholz, Bruno Baur.

Visualization: Ramona Laila Melliger, Brigitte Braschler, Hans-Peter Rusterholz.

Writing – original draft: Ramona Laila Melliger, Brigitte Braschler.

Writing – review & editing: Hans-Peter Rusterholz, Bruno Baur.

References

1. Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, et al. Global change and the ecology of cities. Science. 2008; 319: 756–760. https://doi.org/10.1126/science.1150195 PMID: 18258902
2. Niemelä J. Ecology and urban planning. Biodivers Conserv. 1999; 8: 119–131. https://doi.org/10.1023/A:1008817325994
3. McKinney ML. Urbanization, biodiversity and conservation. BioScience. 2002; 52: 883–890. https://doi.org/10.1043/0006-3568(2002)052(0883:UBAC)2.0.CO;2
4. Gilbert OL. Städtische Ökosysteme. Radebeul: Neumann; 1994.
5. Pickett STA, Cadenasso ML, Grove JM, Boone CG, Groffman PM, Irwin E, et al. Urban ecology systems: scientific foundations and a decade of progress. J Environ Manage. 2011; 92: 331–362. https://doi.org/10.1016/j.jenvman.2010.08.022 PMID: 20965643
6. Sukopp H. Urban ecology: scientific and practical aspects. In: Breuste J, Feldmann H, Uhlmann O (eds), Urban Ecology. Berlin: Springer; 1998. pp. 3–16.
7. Concepción ED, Moretti M, Altermatt F, Nobis MP, Obrist MK. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos. 2015; 124: 1571–1582. https://doi.org/10.1111/oik.02166

8. Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, et al. Biotic control over the functioning of ecosystems. Science. 1997; 277: 500–504. https://doi.org/10.1126/science.277.5325.500
9. Bradley CA, Altizer S. Urbanization and the ecology of wildlife diseases. Trends Ecol. Evol. 2007; 22: 95–102. https://doi.org/10.1016/j.tree.2006.11.001 PMID: 17113678
10. Sitko J, Zaleśny G. The effect of urbanization on helminth communities in the Eurasian blackbird (Turdus merula L.) from the eastern part of the Czech Republic. J. Helminthology. 2014; 88: 97–104. https://doi.org/10.1017/S0022149X12000818 PMID: 23232073
11. Máximo HJ, Felizatti HL, Ceccato M, Cintra-Socolowski P, Beretta ALRZ. Ants as vector of pathogenic microorganisms in a hospital in Sao Paulo county, Brazil. BMC Research Notes 2014; 7:554. https://doi.org/10.1186/1756-0500-7-554 PMID: 25142795
12. Godefroid S, Koedam N. Urban plant species patterns are highly driven by density and function of built-up areas. Landscape Ecol. 2007; 22: 1227–1239. https://doi.org/10.1007/s10980-007-9102-x
13. Kühn I, Brandl R, Klotz S. The flora of German cities is naturally species rich. Evol Ecol Res. 2004; 6: 749–764
14. Cvejić R, Eler K, Pintar M, Železnikar Š, Haase D, Kabisch N, Strohbach Met al. D3.1 A typology of urban green spaces, ecosystem services provisioning services and demands. Work package 3. 2015;
15. Bolund P, Hunhammer S. Ecosystem services in urban areas. Ecol Econ. 1999; 29: 293–301. https://doi.org/10.1016/S0921-8009(99)00013-0
16. Croci S, Butet A, Georges A, Aguejdad R, Clergeau P. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landscape Ecol. 2008; 23: 1171–1186. https://doi.org/10.1007/s10980-008-9257-0
17. Horák J, Rom J, Rada P, Šafářová L, Koudelková J, Zasadil P et al. Renaissance of a rural artifact in a city with a million people: biodiversity responses to an agro-forestry restoration in a large urban traditional fruit orchard. Urban Ecosyst. 2018; online available. doi.org/10.1007/s11252-017-0712-z
18. Kowarik I, Buchholz S, von der Lippe M, Seitz B. Biodiversity functions of urban cemeteries: Evidence from one of the largest Jewish cemeteries in Europe. Urban Forest. Urban Green. 2016; 19: 68–78. doi.org/10.1016/j.ufug.2016.06.023
19. McIntyre NE, Rango J, Fagan WF, Faeth SH. Ground arthropod community structure in a heterogeneous urban environment. Landscape Urban Plan. 2001; 52: 257–274. https://doi.org/10.1016/S0169-2046(00)00122-5
20. Lizée M-H, Mauffrey J-F, Tatoni T, Dechamps-Cottin M. Monitoring urban environments on the basis of biological traits. Ecol Indic. 2011; 11: 353–361. https://doi.org/10.1016/j.ecolind.2010.06.003
21. Gibb H, Hochuli DF. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv. 2002; 106: 91–100. https://doi.org/10.1016/S0006-3207(01)00232-4
22. Magura T, Tóthmérész B, Molnár T. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecol. 2004; 19: 747–759. https://doi.org/10.1007/s10980-005-1128-4
23. Holt RD, Lawton JH, Polis GA, Martinez ND. Trophic rank and the species–area relationship. Ecology. 1999; 80: 1495–1504. https://doi.org/10.1890/0012-9658(1999)080[1495:TRATSA]2.0.CO;2
24. Steffan-Dewenter I. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv Biol. 2003; 17: 1036–1044. https://doi.org/10.1046/j.1523-1739.2003.01575.x
25. Vallet J, Beaujouan V, Pithon J, Rozé F, Daniel H. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. Biodivers Conserv. 2010; 19: 3375–3392. https://doi.org/10.1007/s10531-010-9901-2
26. Gaublomme E, Hendrickx F, Dhuyvetter H, Desender K. The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biol. Conserv. 2008; 141: 2585–2596. https://doi.org/10.1016/j.biocon.2008.07.022
27. Chace JF, Walsh JJ. Urban effects on native avifauna: a review. Landscape Urban Plan. 2006; 74: 46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007
28. McKinney ML. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 2008; 11: 161–176. https://doi.org/10.1007/s11252-007-0045-4
29. Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ. Arthropods in urban habitat fragments in Southern California: Area, age, and edge effects. Ecol. Appl. 2000; 10: 1230–1248. https://doi.org/10.1890/1051-0761(2000)010[1230:AIUHFI]2.0.CO;2

30. Rota E, Caruso T, Migliorini M, Monaci F, Agamennone V, Biagini G et al. Diversity and abundance of soil arthropods in urban and suburban holm oak stands. Urban Ecosyst. 2015; 18: 715–728. https://doi.org/10.1007/s11252-014-0425-5
31. Deichsel R. Species change in an urban setting–ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin. Urban Ecosyst. 2006; 9: 161–178. https://doi.org/10.1007/s11252-006-8588-3
32. Vergnes A, Pellissier V, Lemperiere G, Rollard C, Clergeau P. Urban densification causes the decline of ground-dwelling arthropods. Biodivers Conserv. 2014; 23: 1859–1877. https://doi.org/10.1007/s10531-014-0689-3
33. Fujita A, Maeto K, Kagawa Y, Ito N. Effects of forest fragmentation on species richness and composition of ground beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. Entomol. Science. 2008; 11: 39–48. https://doi.org/10.1111/j.1479-8298.2007.00243.x
34. Gibbs JP, Stanton EJ. Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. Ecol. Appl. 2001; 11: 79–85. https://doi.org/10.1890/1051-0761(2001)011[0079:HFAACC]2.0.CO;2
35. Melliger RL, Rusterholz H-P, Baur B. Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape. Urban Ecosyst. 2017; 20: 1095–1107. https://doi.org/10.1007/s11252-017-0662-5
36. McDonnell MJ, Hahs AK. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecol. 2008; 23: 1143–1155. https://doi.org/10.1007/s10980-008-9253-4
37. Burnand J, Hasspacher B. Waldstandorte beider Basel. Quellen und Forschungen zur Geschichte und Landeskunde des Kantons Basel-Landschaft, Band 72. Verlag des Kantons Basel-Landschaft; 1999.
38. Gyenizse P, Bognár Z, Czigány S, Elekes T. Landscape shape index, as a potential indicator of urban development in Hungary. Landsc Environ. 2014; 8: 78–88
39. Braun-Blanquet J. Pflanzensoziologie: Grundzüge der Vegetationskunde. New York: Springer; 1964.
40. Seifert B. Die Ameisen Mittel- und Nordeuropas. Görlitz: Lutra; 2007.
41. Ward PS, Blaimer BB, Fisher BL. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. Zootaxa. 2016; 4072: 343–357. https://doi.org/10.11646/zootaxa.4072.3.4 PMID: 27395929
42. Roberts MJ. The spiders of Great Britain and Ireland, Volume 1: Atypidae to Theridiosomatidae. Colchester: Harley Books; 1985.
43. Roberts MJ. The spiders of Great Britain and Ireland, Volume 2: Linyphiidae and checklist. Colchester Harley: Books; 1987.
44. Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C. Spiders of Europe. 2017; http://www.araneae.unibe.ch, ver. 03.2017. 10.24436/1
45. Schuler J. Baumbewohnende Ameisen mitteleuropäischer Auenwälder. Artenspektrum und Ökologie arborikoler Ameisen in naturnahen Hartholzauen an Rhein, Elbe und Donau. Zürich: Bristol-Stiftung; Bern: Haupt; 2015.
46. Delarze R, Gonseth Y, Eggenberg S. Lebensräume der Schweiz: Ökologie–Gefährdung–Kennarten, 3rd edn. Bern: Ott Verlag; 2015.
47. Hänggi A, Stöckli E, Nentwig W. Lebensräume Mitteleuropäischer Spinnen. Neuchâtel: Miscellanea Faunistica Helvetiae 4. Centre de cartographie de la faune (CSCF); 1995.
48. Grime JP. Plant strategies and vegetation processes. Chichester: Wiley; 1979.
49. Klotz S, Kühn I, Durka W. BIOLFLOR–Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bonn: LandWirtschaftsverlag. 2002; http://www2.ufz.de/biolflor (accessed 9 May 2017)
50. Müller-Schneider P. Verbreitungsbiologie der Blütenpflanzen Graubündens, 85. Heft. Veröffentl. Geobot. Inst. ETH, Zurich: Stiftung Rübel; 1986.
51. Wiki der Arachnologischen Gesellschaft e.V. 'Hauptseite'. 2017; https://wiki.arages.de/index.php?title=Hauptseite&oldid=91730 (accessed 23 May 2017)
52. Allen SE. Chemical analysis of ecological material, 2nd ed. Oxford: Blackwell Scientific; 1989.
53. Bremner JM. Total nitrogen. In: Black C.A. (ed), Methods of soil analysis, Part 2. Madison: American Society of Agronomy; 1965. pp. 1149–1178.
54. Sparks DL, Page AL, Helmke PA, Loeppert RA, Soltanpour PN, Tabatabai MA, et al. Methods of soil analysis Part 3 –Chemical methods, 3rd ed. Madison: SSSA; 1996. https://doi.org/10.2136/sssabookser5.3.c32

55. Godínez-Alvarez H, Herrick JE, Mattocks M, Toledo D, Van Zee J. Comparison of three vegetation monitoring methods: their relative utility for ecological assessment and monitoring. Ecol Indic. 2009; 9: 1001–1008. https://doi.org/10.1016/j.ecolind.2008.11.011

56. Melliger RL, Rusterholz H-P, Baur B. Ecosystem functioning in cities: Combined effects of urbanization and forest size on early-stage leaf litter decomposition of European beech (*Fagus sylvatica* L.). Urban For. Urban Green. 2017; 28: 88–96. https://doi.org/10.1016/j.ufug.2017.10.009

57. Hothorn T, Bretz F, Westfall P. Simultaneous inference in general parametric models. Biometr. J. 2008; 50: 346–363. https://doi.org/10.1002/bimj.200810425 PMID: 18481363

58. Bray JR, Curtis JT. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 1957; 27: 325–349. https://doi.org/10.2307/1942268

59. Anderson MJ. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand. 2005.

60. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. Vegan: community ecology package. R package version 2.4–2. 2017. https://CRAN.R-project.org/package=vegan

61. Villéger S, Mason NW, Mouillot D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology. 2008; 89: 2290–2301. https://doi.org/10.1890/07-1206.1 PMID: 18724739

62. Laliberté E, Legendre P, Shipley B. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12. 2014.

63. Cameron GN, Culley TM, Kolbe SE, Miller AI, Matter SF. Effects of urbanization on herbaceous forest vegetation: the relative impacts of soil, geography, forest composition, human access, and an invasive shrub. Urban Ecosyst. 2015; 18: 1051–1069. https://doi.org/10.1007/s11252-015-0472-6

64. Alaruikka D, Kotze DJ, Matveinen K, Niemelä J. Carabid beetle and spider assemblages along a forested urban–rural gradient in southern Finland. J Insect Conserv. 2002; 6: 195–206. https://doi.org/10.1023/A:1024432830064

65. Magura T, Horváth R, Tóthmérész B. Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary. Landscape Ecol. 2010; 25: 621–629. https://doi.org/10.1007/s10980-009-9445-6

66. Horváth R, Magura T, Tóthmérész B. Ignoring ecological demands masks the real effect of urbanization: a case study of ground-dwelling spiders along a rural–urban gradient in a lowland forest in Hungary. Ecol Res. 2012; 27: 1069–1077. https://doi.org/10.1007/s11284-012-0988-7

67. Aubin I, Venier L, Pearce J, Moretti M (2013) Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity? Biodivers Conserv. 2013; 22: 2957–2975. https://doi.org/10.1007/s10531-013-0565-6

68. Didham RK, Ghazoul J, Stork NE, Davis AJ. Insects in fragmented forests: a functional approach. Trends Ecol Evol. 1996; 11: 255–260. https://doi.org/10.1016/0169-5347(96)20047-3 PMID: 21237834

69. MacArthur RH, Wilson EO. The theory of island biogeography. New Jersey: Princeton University Press; 1967.

70. Hobbs ER. Species richness of urban forest patches and implications for urban landscape diversity. Landscape Ecol. 1988; 1: 141–152. https://doi.org/10.1007/BF00162740

71. Godefroid S, Koedam N. How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? Global Ecol Biogeogr. 2003; 12: 287–298. https://doi.org/10.1046/j.1466-822X.2003.00035.x

72. Miyashita T, Shinkaib A, Chidac T. The effects of forest fragmentation on web spider communities in urban areas. Biol Conserv. 1998; 86: 357–364. https://doi.org/10.1016/S0006-3207(98)00025-1

73. Ivanov K, Keiper J. Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. Biodivers Conserv. 2010; 19: 3917–3933. https://doi.org/10.1007/s10531-010-9937-3

74. Bengtsson J, Lundkvist H, Saetre P, Sohlenius B, Solbreck B. Effects of organic matter removal on the soil food web: forestry practices meet ecological theory. Appl Soil Ecol. 1998; 9: 137–143. https://doi.org/10.1016/S0929-1393(98)00067-5

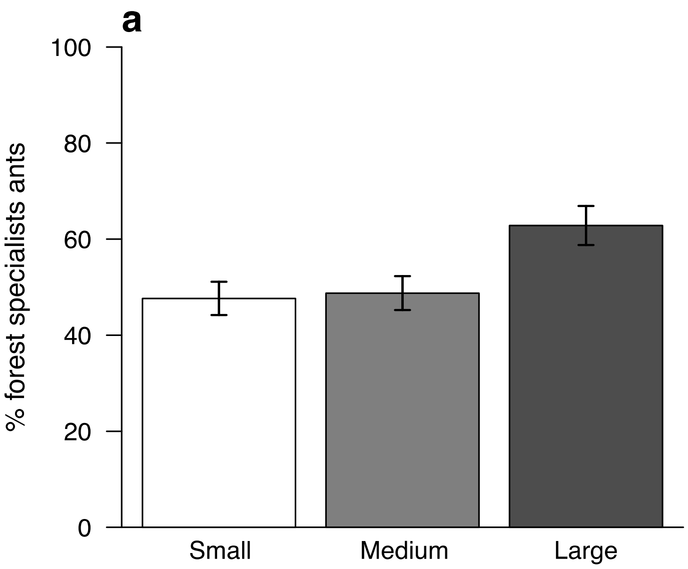
75. Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hasting A, et al. Detritus, trophic dynamics and biodiversity. Ecol Lett. 2004; 7: 584–600. https://doi.org/10.1111/j.1461-0248.2004.00606.x

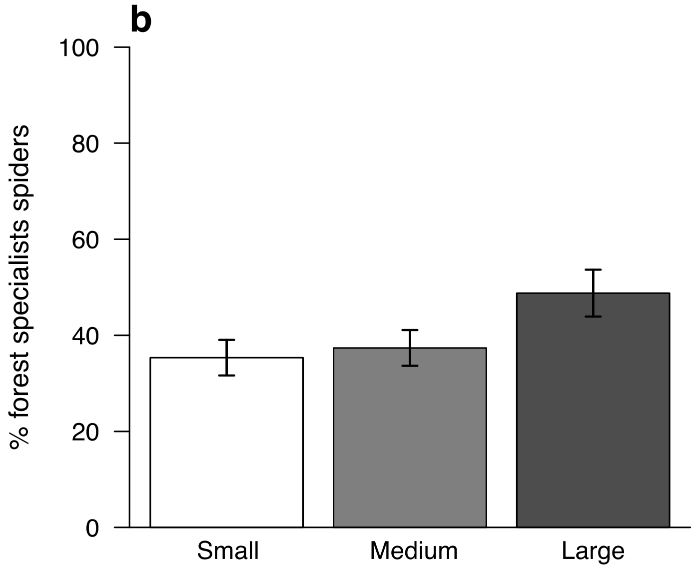
76. Mason NWH, Mouillot D, Lee WG, Wilson JB. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos. 2005; 111: 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

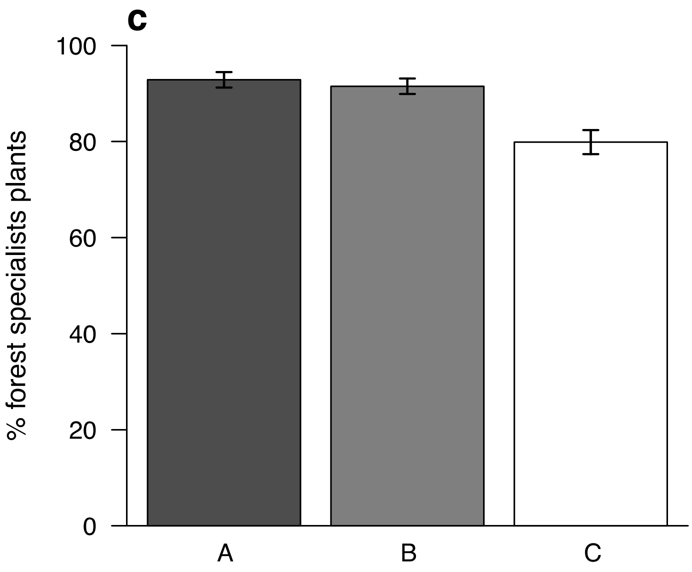
Supplementary material Chapter II

S1 Figure	Forest specialists in relation to size and shape of urban forests
S1 Table	Description of forest sites
S2 Table	Landscape, forest and plot characteristics recorded during field surveys
S3 Table	Species and trait lists
S4 Table	Correlations within and among landscape and site characteristics
S5 Table	Species–site matrices for plants, ants and spiders
S6 Table	Data used to perform PERMANOVA
S7 Table	Percentage of sites in which common species occur for different degrees of urbanisation and forest size classes
S8 Table	Functional dispersion: Summary of ANCOVAs of plants
S9 Table	Functional dispersion: Summary of ANCOVAs of ants and spiders

S1 Fig. Forest specialists in relation to size and shape of urban forests. Percentage forest specialist species of a) ants and b) spiders in fragments of different size; size classes are small (< 4000 m^2), medium-sized (4000–10,000 m^2) and large (> 10,000 m^2); and c) percentage of forest specialist species of plants depending on the shape of the fragment. The shape index was calculated following Gyenizse et al. [28]. A shape index of 1 corresponds to a circular area, which is considered as most stable and resistant against biotic and abiotic effects from the surrounding landscape. Classes are A: continuous forest, B: shape index between 1 and 1.5, C: shape index > 1.5.






c
% forest specialists plants
0
20
40
60
80
100
A
B
C

S1 Table. Description of forest sites. Characteristics of the 26 forests examined in Basel (Switzerland) and its surroundings.

Forest	Coordinates	Historical development	Elevation (m a.s.l.)	Exposure	Area (m^2)	Shape index	% cover of sealed area (r = 200 m)	% cover of sealed area (r = 500 m)	Time since last thinning (in y)	Path density (m/ha)	Mean canopy closure (in %)
BS1	47° 34' 34.58" N 7° 36' 19.23" E	Forest	269	–	21000	Continuous	4	20	2	360.6	97.81
BS2	47° 34' 20.76" N 7° 36' 52.84" E	Planted	263	–	620	1.25	22	22	7	580.6	98.18
BS3	47° 34' 20.65" N 7° 37' 11.82" E	Planted	265	–	4576	1.64	10	12	9	243.2	97.39
BS4	47° 33' 45.65" N 7° 37' 44.02" E	Planted	262	S	7458	3.39	12	19	> 20	311.6	94.67
BS5	47° 33' 12.30" N 7° 36' 51.09" E	Planted	262	NE	7049	2.26	39	39	3	283.7	92.47
BS6	47° 32' 43.72" N 7° 36' 26.85" E	Planted	276	–	1084	1.20	69	70	14	48.0	97.80
BS7	47° 32' 8.70" N 7° 35' 23.09" E	Fragment	326	E	3009	2.91	32	30	1	254.6	94.63
BS8	47° 32' 17.69" N 7° 35' 38.71" E	Planted	303	N	2285	1.42	34	43	3	337.0	96.02
BS9	47° 32' 12.27" N 7° 36' 5.97" E	Fragment	321	NE	3244	1.22	39	54	8	334.8	96.77
BS10	47° 31' 57.55" N 7° 36' 11.58" E	Fragment	338	NW	14000	1.29	29	44	6	445.9	98.26
BS11	47° 31' 47.76" N 7° 35' 49.19" E	Fragment	370	SE	21000	1.32	19	23	9	410.3	95.44
BS12	47° 31' 26.26" N 7° 35' 33.76" E	Fragment	314	–	19400	2.12	9	14	4	319.1	94.99
BS13	47° 31' 46.44" N 7° 36' 12.24" E	Planted	376	NW	3633	2.35	28	46	16	715.7	98.28

Forest	Coordinates	Historical development	Elevation (m a.s.l.)	Exposure	Area (m^2)	Shape index	% cover of sealed area (r = 200 m)	% cover of sealed area (r = 500 m)	Time since last thinning (in y)	Path density (m/ha)	Mean canopy closure (in %)
BS14	47° 35' 33.14” N 7° 40' 41.10” E	Forest	473	SW	34000	Continuous	1	3	> 20	23	96.19
BS15	47° 35' 15.09” N 7° 40' 2.90” E	Planted	346	S	2800	2.81	6	10	7	114.3	97.38
BS16	47° 35' 5.71” N 7° 40' 9.23” E	Planted	330	S	4061	1.88	9	8	3	448.2	97.28
BS17	47° 35' 18.09” N 7° 38' 52.08” E	Planted	273	–	258	1.12	3	17	> 20	658.9	92.54
BS18	47° 34' 30.78” N 7° 40' 35.28” E	Forest	487	–	14000	Continuous	1	4	1	80	92.11
BS19	47° 34' 25.90" N 7° 39' 53.22" E	Forest	450	NW	50000	1.10	7	10	> 20	151.4	95.58
BS20	47° 34' 29.73" N 7° 39' 29.56" E	Fragment	384	NW	36000	1.24	13	12	11	557.6	97.86
BS21	47° 34' 51.72" N 7° 39' 37.41" E	Fragment	302	–	4686	1.19	8	16	15	200.6	94.50
BS22	47° 34' 53.45" N 7° 38' 51.87" E	Planted	283	–	5765	1.14	43	33	16	582.2	97.99
BS23	47° 34' 0.42" N 7° 38' 22.88" E	Planted	277	–	4234	1.79	24	24	1	571.6	92.03
BS24	47° 33' 58.73" N 7° 38' 46.35" E	Planted	309	S	1500	2.64	24	14	1	0	94.23
BS25	47° 33' 50.63" N 7° 38' 42.82" E	Forest	319	NW	4034	Continuous	8	12	1	210.7	95.22
BS26	47° 34' 7.38" N 7° 39' 4.87" E	Forest	363	NW	8908	Continuous	10	12	2	264.6	92.32

S2 Table Landscape, forest and plot characteristics recorded during field surveys https://doi.org/10.1371/journal.pone.0199245.s002

S3 Table. Species and trait lists. Species list of (a) vascular plants, (b) ants and (c) spiders. Habitat specificity, conservation status (Red List) and a set of traits, which we considered to influence species' response to urbanisation-related factors are shown. Traits not used for analyses are in parentheses.

a) Vascular plants

Species	**Habitat specificity**[1]	**Red List**[2]	**Plant life form**[3]	**Reproduction type**[3]	**Ecological strategy**[3, 4]	**Pollination syndrome**[3]	**Seed dispersal type**[5]	**Mean seed mass (mg)**[3]
Acer campestre L.	Forest species	LC	Macrophanerophyte	Mixed	C	Insects	Anemochory	96.8
Acer platanoides L.	Forest species	LC	Macrophanerophyte	Sexual	C	Insects	Anemochory	137.2
Acer pseudoplatanus L.	Forest species	LC	Macrophanerophyte	Sexual	C	Insects	Anemochory	110.7
Aegopodium podagraria L.	Forest species	LC	Hemicryptophyte	Mixed	C	Insects	Hemerochory	2.2
Aesculus hippocastanum L.	Forest species	LC	Macrophanerophyte	Sexual	C	Insects	Zoochory	10612
Agrostis capillaris L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Wind	Anemochory	0.1
Agrostis gigantea Roth	Forest species	LC	Hemicryptophyte	Mixed	C	Wind	Anemochory	0.1
Ailanthus altissima (Mill.) Swingle	Forest species	LC	Macrophanerophyte	Mixed	C	Insects	Anemochory	33.6
Alliaria petiolata (M. Bieb.) Cavara & Grande	Non-forest species	LC	Hemicryptophyte	Sexual	CR	Insects	Anemochory	2.3
Allium sp.	–	LC	–	–	–	Insects	–	–
Allium ursinum L.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Zoochory	7.3
Anemone nemorosa L.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Zoochory	2.6
Arum maculatum L.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Zoochory	41.0
Berberis julianae C.K. Schneid.	Non-forest species	LC	Nanophanerophyte	–	–	Insects	Zoochory	–
Berberis vulgaris L.	Non-forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	11.9
Borago officinalis L.	Non-forest species	LC	Hemicryptophyte	Sexual	CR	Insects	Zoochory	15.5
Brachypodium pinnatum aggr.	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	2.8
Brachypodium sylvaticum (Huds.) P. Beauv.	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	0.6

Species	Habitat specificity[1]	Red List[2]	Plant life form[3]	Reproduction type[3]	Ecological strategy[3, 4]	Pollination syndrome[3]	Seed dispersal type[5]	Mean seed mass (mg)[3]
Buxus sempervirens L.	Forest species	NT	Nanophanerophyte	Sexual	CS	Insects	Anemochory	–
Calystegia sepium (L.) R. Br.	Non-forest species	LC	Geophyte	Mixed	C	Insects	Autochory	31.3
Carex muricata aggr.	–	LC	Hemicryptophyte	Mixed	C	Wind	Zoochory	2.1
Carex pendula Huds.	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	0.8
Carex remota L.	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	0.3
Carex sylvatica Huds.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Wind	Zoochory	1.4
Carpinus betulus L.	Forest species	LC	Macrophanerophyte	Mixed	C	Wind	Anemochory	63.8
Castanea sativa Mill.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	–
Circaea lutetiana L.	Forest species	LC	Geophyte	Mixed	CS	Insects	Zoochory	2.0
Clematis vitalba L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Anemochory	2.8
Cornus sanguinea L.	Forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	35.2
Corylus avellana L.	Forest species	LC	Nanophanerophyte	Mixed	C	Wind	Zoochory	1042.0
Cotoneaster integerrimus Medik.	Forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	9.7
Cotoneaster tomentosus Lindl.	Non-forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	13.3
Crataegus laevigata (Poir.) DC.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	40.8
Crataegus monogyna Jacq.	Non-forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	64.9
Dactylis glomerata L.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Wind	Anemochory	0.6
Dactylis polygama Horv.	Forest species	NT	Hemicryptophyte	Sexual	CS	Wind	Anemochory	–
Daphne laureola L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	103.4
Dryopteris filix-mas (L.) Schott	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	–
Duchesnea indica (Andrews) Focke	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	0.4
Epilobium montanum L.	Forest species	LC	Hemicryptophyte	Mixed	CS	Insects	Anemochory	0.1
Epilobium parviflorum Schreb.	Non-forest species	LC	Hemicryptophyte	Mixed	CS	Insects	Anemochory	0.1
Euonymus europaeus L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	33.0
Euphorbia amygdaloides L.	Forest species	LC	Chamaephyte	Mixed	CS	Insects	Zoochory	4.6
Fagus sylvatica L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	254.0
Festuca ovina aggr.	Non-forest species	LC	Hemicryptophyte	Sexual	CSR	Wind	Anemochory	0.3

Species	Habitat specificity[1]	Red List[2]	Plant life form[3]	Reproduction type[3]	Ecological strategy[3, 4]	Pollination syndrome[3]	Seed dispersal type[5]	Mean seed mass (mg)[3]
Festuca rubra aggr.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Wind	Anemochory	0.8
Filipendula ulmaria (L.) Maxim.	Forest species	LC	Hemicryptophyte	Mixed	C	Insects	Anemochory	0.7
Fragaria vesca L.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	0.3
Fraxinus excelsior L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Anemochory	77.4
Galeopsis tetrahit L.	Forest species	LC	Therophyte	Sexual	CR	Insects	Zoochory	4.6
Galium mollugo aggr.	Non-forest species	LC	Hemicryptophyte	Sexual	C	Insects	Zoochory	0.5
Galium odoratum (L.) Scop.	Forest species	LC	Geophyte	Mixed	S	Insects	Zoochory	8.2
Galium spurium L.	Non-forest species	VU	Therophyte	Sexual	CR	Insects	Zoochory	2.7
Geranium robertianum L. s.l.	Forest species	LC	Therophyte	Sexual	CSR	Insects	Autochory	1.1
Geum urbanum L.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	2.4
Glechoma hederacea L. s.l.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	0.7
Hedera helix L.	Forest species	LC	Nanophanerophyte	Mixed	CS	Insects	Zoochory	20.4
Helictotrichon pubescens (Huds.) Pilg.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Wind	Anemochory	1.9
Helleborus foetidus L.	Forest species	LC	Chamaephyte	Sexual	CS	Insects	Zoochory	11.4
Heracleum sphondylium L. s.l.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Insects	Anemochory	5.9
Hypericum hirsutum L.	Forest species	LC	Hemicryptophyte	Sexual	C	Insects	Anemochory	0.1
Hypericum perforatum L. s.l.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Insects	Anemochory	0.1
Ilex aquifolium L.	Forest species	LC	Macrophanerophyte	Mixed	C	Insects	Zoochory	140.0
Impatiens parviflora DC.	Forest species	LC	Therophyte	Sexual	SR	Insects	Autochory	7.4
Juglans regia L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	6500.0
Lamium galeobdolon subsp. *argentatum* (Smejkal) J. Duvign.	–	LC	Chamaephyte	Mixed	CS	Insects	Zoochory	–
Lamium galeobdolon subsp. *montanum* (Pers.) Hayek	Forest species	LC	Chamaephyte	Mixed	CS	Insects	Zoochory	1.8
Lathyrus vernus (L.) Bernh. s.l.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Autochory	15.2
Leontodon hispidus L. s.l.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Anemochory	0.8
Ligustrum vulgare L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	20.4
Lolium multiflorum Lam.	Non-forest species	LC	Hemicryptophyte	Sexual	C	Wind	Anemochory	2.4
Lonicera henryi Hemsl.	Forest species	LC	Nanophanerophyte	–	–	Insects	Zoochory	–

Species	Habitat specificity[1]	Red List[2]	Plant life form[3]	Reproduction type[3]	Ecological strategy[3, 4]	Pollination syndrome[3]	Seed dispersal type[5]	Mean seed mass (mg)[3]
Lonicera pileata Oliv.	–	LC	Nanophanerophyte	–	–	Insects	Zoochory	–
Lonicera xylosteum L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	–
Luzula sylvatica (Huds.) Gaudin	Forest species	LC	Hemicryptophyte	Mixed	C	Wind	Zoochory	0.7
Mahonia aquifolium (Pursh) Nutt.	Forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	9.3
Maianthemum bifolium (L.) F.W. Schmidt	Forest species	LC	Geophyte	Mixed	S	Insects	Zoochory	11.7
Medicago lupulina L.	Non-forest species	LC	Therophyte	Mixed	CSR	Insects	Zoochory	1.6
Melica nutans L.	Forest species	LC	Hemicryptophyte	Mixed	CS	Wind	Anemochory	2.0
Melittis melissophyllum L.	Forest species	LC	Hemicryptophyte	Mixed	C	Insects	Zoochory	–
Origanum vulgare L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Anemochory	0.1
Paris quadrifolia L.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Zoochory	4.0
Phyllitis scolopendrium (L.) Newman	Forest species	LC	Hemicryptophyte	Sexual	CS	Wind	Anemochory	–
Phyteuma spicatum L.	Forest species	LC	Hemicryptophyte	Sexual	CSR	Insects	Anemochory	0.2
Picea abies (L.) H. Karst.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	7.2
Plantago lanceolata L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Wind	Zoochory	1.8
Poa pratensis L.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Wind	Zoochory	0.3
Poa trivialis L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Wind	Zoochory	0.1
Polygonatum multiflorum (L.) All.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Zoochory	22.1
Potentilla reptans L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	0.3
Potentilla sp.	–	LC	–	–	–	Insects	–	–
Primula elatior (L.) L.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Anemochory	0.9
Prunus avium L.	Forest species	LC	Macrophanerophyte	Sexual	C	Insects	Zoochory	170.0
Prunus domestica L.	–	LC	Macrophanerophyte	Mixed	C	Insects	Zoochory	–
Prunus laurocerasus L.	Forest species	LC	–	–	–	Insects	Zoochory	–
Prunus padus L. s.l.	Forest species	LC	Macrophanerophyte	Mixed	C	Insects	Zoochory	50.0
Prunus serotina Ehrh.	Forest species	LC	Macrophanerophyte	Mixed	C	Insects	Zoochory	–
Prunus spinosa L.	Non-forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	145.2
Pulmonaria officinalis aggr.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	–

Species	Habitat specificity[1]	Red List[2]	Plant life form[3]	Reproduction type[3]	Ecological strategy[3, 4]	Pollination syndrome[3]	Seed dispersal type[5]	Mean seed mass (mg)[3]
Quercus petraea Liebl.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	774.6
Quercus robur L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	–
Quercus rubra L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	2694.0
Ranunculus auricomus L.	Forest species	LC	–	–	CSR	Insects	Anemochory	–
Ranunculus ficaria L.	Forest species	LC	Geophyte	Mixed	CSR	Insects	Hemerochory	1.0
Ribes rubrum L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	9.2
Ribes uva-crispa L.	Non-forest species	LC	Nanophanerophyte	Mixed	C	Insects	Zoochory	–
Rosa sp.	Forest species	LC	Nanophanerophyte	–	–	Insects	Zoochory	–
Rubus sp.	Forest species	LC	–	–	–	Insects	Zoochory	–
Rumex sp.	–	LC	Hemicryptophyte	–	–	Wind	Anemochory	–
Sambucus nigra L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	3.2
Solidago canadensis aggr.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Insects	Anemochory	0.1
Sorbus x Sorbopyrus	–	LC	–	–	–	Insects	–	–
Stachys sylvatica L.	Forest species	LC	Hemicryptophyte	Mixed	CS	Insects	Zoochory	1.6
Stellaria media aggr.	Non-forest species	LC	Therophyte	Sexual	CR	Insects	Anemochory	0.5
Tanacetum sp.	Non-forest species	LC	–	–	–	Insects	–	–
Taraxacum officinale aggr.	Non-forest species	LC	Hemicryptophyte	Sexual	CSR	Insects	Anemochory	0.7
Taxus baccata L.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Zoochory	51.6
Tilia platyphyllos Scop.	Forest species	LC	Macrophanerophyte	Sexual	C	Insects	Anemochory	112.0
Trifolium repens L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Zoochory	0.6
Ulmus glabra Huds.	Forest species	LC	Macrophanerophyte	Sexual	C	Wind	Anemochory	12.5
Urtica dioica L.	Forest species	LC	Hemicryptophyte	Mixed	C	Wind	Anemochory	0.1
Veronica chamaedrys L.	Non-forest species	LC	Chamaephyte	Mixed	CSR	Insects	Anemochory	0.2
Veronica montana L.	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Anemochory	0.3
Veronica serpyllifolia L.	Non-forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Hydrochory	0.1
Viburnum lantana L.	Forest species	LC	Nanophanerophyte	Sexual	CS	Insects	Zoochory	–
Viburnum opulus L.	Forest species	LC	Nanophanerophyte	Sexual	C	Insects	Zoochory	25.5

Species	Habitat specificity[1]	Red List[2]	Plant life form[3]	Reproduction type[3]	Ecological strategy[3, 4]	Pollination syndrome[3]	Seed dispersal type[5]	Mean seed mass (mg)[3]
Viburnum rhytidophyllum Hemsl.	–	LC	–	–	–	Insects	Zoochory	–
Vicia cracca L. s.l.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Insects	Autochory	14.3
Vicia sepium L.	Non-forest species	LC	Hemicryptophyte	Mixed	C	Insects	Autochory	21.4
Viola reichenbachiana Boreau	Forest species	LC	Hemicryptophyte	Mixed	CSR	Insects	Autochory	4.0

[1] Delarze, R. et al. 2015. Lebensräume der Schweiz, 3rd edn. – Ott Verlag.

[2] Red list of vascular plants: Bornand, C. et al. 2016. Rote Liste Gefässpflanzen. Gefährdete Arten der Schweiz. – Bundesamt für Umwelt, Bern und Info Flora, Genf. Umwelt-Vollzug Nr. 1621. Threat categories are: LC = least concern, NT = near threatened, VU = vulnerable

[3] Klotz, S. et al. 2002. BIOLFLOR – Eine Datenbank mit Biologisch-Ökologischen Merkmalen zur Flora von Deutschland. – LandWirtschaftsverlag, Bonn. <http://www2.ufz.de/biolflor> accessed 10 May 2017.

[4] Ecological strategy following 'Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley': C = competitive, S = stress tolerant, R = ruderal

[5] Müller-Schneider, P. 1986. Verbreitungsbiologie der Blütenpflanzen Graubündens 85. Heft. – Veröffentl Geobot Inst ETH, Stiftung Rübel.

b) Ants

Species	Habitat specifity[1]	Red List[2]	Subfamily	Body size (mm)[3]	Number of queens[4]	Main Food[5]	Main nest stratum[6]
Aphaenogaster subterranea (Latreille 1798)	Forest species	VU	Myrmicinae	5	–	Carbohydrates & animal matter	Soil & crevices
Colobopsis truncata (Spinola 1808)	Forest species		Formicinae	4	Monogynous	Carbohydrates & animal matter	Wood & litter
Dolichoderus quadripunctatus (Linnaeus 1771)	Forest species		Dolichoderinae	4	Monogynous	Carbohydrates	Wood & litter
Formica cunicularia Latreille 1798	Open-land species		Formicinae	7.5	Monogynous	Carbohydrates & animal matter	Soil & crevices
Formica fusca Linnaeus 1758	Generalist		Formicinae	7	Polygynous	Carbohydrates & animal matter	Soil & crevices
Formica rufibarbis Fabricius 1793	Open-land species		Formicinae	7.5	Polygynous	Animal matter	Soil & crevices
Lasius brunneus (Latreille 1798)	Forest species		Formicinae	4.5	Monogynous	Carbohydrates	Wood & litter
Lasius emarginatus (Olivier 1792)	Open-land species		Formicinae	4.5	Monogynous	Carbohydrates & animal matter	Soil & crevices
Lasius flavus (Fabricius 1798)	Open-land species		Formicinae	4.8	Oligogynous	Carbohydrates	Soil & crevices
Lasius fuliginosus (Latreille 1798)	Forest species		Formicinae	6	Polygynous	Carbohydrates & animal matter	Wood & litter
Lasius mixtus (Nylander 1846)	Generalist		Formicinae	4.5	Oligogynous	–	Soil & crevices
Lasius myops Forel 1894	Open-land species		Formicinae	3.6	–	Carbohydrates & animal matter	Soil & crevices
Lasius niger (Linnaeus 1758)	Open-land species		Formicinae	5	Monogynous	Carbohydrates & animal matter	Soil & crevices

Species	Habitat specifity[1]	Red List[2]	Subfamily	Body size (mm)[3]	Number of queens[4]	Main Food[5]	Main nest stratum[6]
Lasius platythorax Seifert 1991	Forest species	*	Formicinae	5	Monogynous	Carbohydrates & animal matter	Both
Lasius psammophilus Seifert 1992	Open-land species	*	Formicinae	4	–	Carbohydrates & animal matter	Soil & crevices
Lasius sabularum (Bondroit 1918)	Generalist	*	Formicinae	4.4	–	Carbohydrates	Wood & litter
Myrmecina graminicola (Latreille 1802)	Generalist		Myrmicinae	3.7	Oligogynous	Animal matter	Soil & crevices
Myrmica rubra (Linnaeus 1758)	Generalist		Myrmicinae	6	Polygynous	Carbohydrates & animal matter	Both
Myrmica ruginodis Nylander 1846	Forest species		Myrmicinae	6	Polygynous	Carbohydrates & animal matter	Both
Myrmica sabuleti Meinert 1861	Open-land species		Myrmicinae	5	Polygynous	Carbohydrates & animal matter	Soil & crevices
Myrmica scabrinodis Nylander 1846	Open-land species		Myrmicinae	6	Polygynous	Carbohydrates & animal matter	Soil & crevices
Myrmica schencki Viereck 1903	Open-land species		Myrmicinae	5.5	Polygynous	Animal matter	Soil & crevices
Myrmica specioides Bondroit 1918	Open-land species	VU	Myrmicinae	4.5	Oligogynous	–	Soil & crevices
Solenopsis fugax (Latreille 1798)	Open-land species		Myrmicinae	3	Polygynous	Animal matter	Soil & crevices
Stenamma debile (Förster 1850)	Forest species		Myrmicinae	4.3	Monogynous	Animal matter	Wood & litter
Stenamma striatulum Emery 1895	Forest species	NT	Myrmicinae	3.4	–	–	Wood & litter
Temnothorax affinis (Mayr 1855)	Forest species		Myrmicinae	3.5	Monogynous	Carbohydrates & animal matter	Wood & litter
Tetramorium cf. *caespitum* (Linnaeus 1758)	Open-land species		Myrmicinae	4	Monogynous	Grains[7]	Soil & crevices

---

[1] Forest species here include all species that primarily nest in wood, even if they can also be found in open habitats with single trees present, e.g. orchards.

[2] No recent red list for the ants of Switzerland exists. Red List information in this table thus follows ‘Agosti, D. and Cherix, D. 1994. Rote Liste der gefährdeten Ameisen der Schweiz. In: Duelli, P. (ed.) Rote Listen der gefährdeten Tierarten der Schweiz. – Bundesamt für Umwelt, Wald und Landschaft, Bern. pp. 45–47.’ Threat categories were adjusted in July 2009 to IUCN categories by the Bundesamt für Umwelt <www.bafu.ch> according to the guidelines published on <http://www.artenschutz.ch/rlist.htm#2> assessed 14 July 2017. Threat categories are: NT = near threatened, VU = vulnerable. Species marked with a (*) were not considered as species-level taxa or not yet distinguished from sibling species in the literature cited by Agosti and Cherix (1994) to identify Swiss ants. It is thus likely their status was not evaluated for the Red List, even though they were already described as separate species at the time of publication in papers by Bernhard Seifert published in 1988-1992. This affects *Lasius plathythorax*, *L. psammophilus* and *L. sabularum*. Many other species have changed names since the publication of the original Red List, but their synonymy is clear. *Tetramorium caespitum* as it was defined at the time of the publication of the red list in 1994 is now recognized to constitute several species, not all of which have already been named, and whose distribution in Switzerland is yet incompletely known. Species considered to be not threatened were not entered into the original list, thus there are none classified into a category equivalent to the IUCN category least concern (LC). All species not marked with an asterisk were part of the keys recommended by Agosti and Cherix (1994) and thus all such species not assigned to a threat category were likely considered LC by the authors of this list.

[3] Maximum total length of workers, including major workers, in species where these forage.

[4] We were interested in the maximum number of queens per colony, thus for a species that has colonies that are monogynous and colonies that are oligogynous the latter would be entered.

[5] Carbohydrates include nectar and animal secretions like honeydew, animal matter includes carrion and prey.

[6] Nest substrate categories were combined to avoid small sample sizes. This means that e.g. the category Wood & crevices includes species using either of these substrates or both.

[7] The species also uses carbohydrate and animal matter food resources. However, the categorization reflects,,that it is more granivorous than other species in these communities

c) Spiders

Species	**Family**	**Habitat specificity**[1, 2]	**Red List**[3]	**Mean body size (mm)**[2]	**Hunting mode**[4, 5]
Agyneta rurestris (C.L. Koch, 1836)	Linyphiidae	Generalist	*	2.13	Web building
Alopecosa pulverulenta (Clerck, 1757)	Lycosidae	Open-land species	*	7.00	Hunting
Amaurobius ferox (Walckenaer, 1830)	Amaurobiidae	Generalist	*	9.00	Web building
Anyphaena accentuata (Walckenaer, 1802)	Anyphaenidae	Forest species	*	5.50	Hunting
Apostenus fuscus Westring, 1851	Liocranidae	Generalist	*	3.07	Hunting
Atypus piceus (Sulzer, 1776)	Atypidae	Generalist	V	9.09	Hunting
Centromerus serratus (O.P.-Cambridge, 1875)	Linyphiidae	Generalist	*	1.70	Web building
Centromerus sylvaticus (Blackwall, 1841)	Linyphiidae	Generalist	*	3.75	Web building
Ceratinella brevis (Wider, 1834)	Linyphiidae	Generalist	*	1.80	Web building
Ceratinella scabrosa (O.P.-Cambridge, 1871)	Linyphiidae	Generalist	*	1.90	Web building
Cetonana laticeps (Canestrini, 1868)	Trachelidae	–	*	6.25	–
Cicurina cicur (Fabricius, 1793)	Dictynidae	Generalist	*	6.00	Web building
Clubiona comta (C.L. Koch, 1839)	Clubionidae	Forest species	*	4.29	Hunting
Clubiona terrestris Westring, 1851	Clubionidae	Forest species	*	6.54	Hunting
Cnephalocotes obscurus (Blackwall, 1834)	Linyphiidae	Open-land species	*	1.70	Web building
Coelotes terrestris (Wider, 1834)	Agelenidae	Forest species	*	9.59	Web building
Dicymbium nigrum (Blackwall, 1834)	Linyphiidae	Generalist	*	2.14	Web building
Diplocephalus latifrons (O.P.-Cambridge, 1863)	Linyphiidae	Generalist	*	1.71	Web building
Diplocephalus picinus (Blackwall, 1841)	Linyphiidae	Forest species	*	1.74	Web building
Diplostyla concolor (Wider, 1834)	Linyphiidae	Generalist	*	2.75	Web building
Drassyllus praeficus (L. Koch, 1866)	Gnaphosidae	Open-land species	V	6.50	Hunting
Drassyllus pusillus (C.L. Koch, 1833)	Gnaphosidae	Open-land species	*	4.75	Hunting

Species	**Family**	**Habitat specificity**[1, 2]	**Red List**[3]	**Mean body size (mm)**[2]	**Hunting mode**[4, 5]
Dysdera erythrina (Walckenaer, 1802)	Dysderidae	Generalist	*	8.88	Hunting
Enoplognatha latimana Hippa & Oksala, 1982	Theridiidae	Open-land species	*	4.67	Web building
Enoplognatha ovata (Clerck, 1757)	Theridiidae	Generalist	*	4.87	Web building
Enoplognatha thoracica (Hahn, 1833)	Theridiidae	Generalist	*	3.78	Web building
Entelecara acuminata (Wider, 1834)	Linyphiidae	Generalist	*	2.20	Web building
Episinus truncatus Latreille, 1809	Theridiidae	Generalist	*	5.30	Web building
Erigone atra Blackwall, 1833	Linyphiidae	Generalist	*	2.20	Web building
Erigone dentipalpis (Wider, 1834)	Linyphiidae	Generalist	*	2.33	Web building
Ero furcata (Villers, 1789)	Mimetidae	Generalist	*	3.95	Hunting
Gonatium rubellum (Blackwall, 1841)	Linyphiidae	Forest species	*	3.20	Web building
Gongylidium rufipes (Linnaeus, 1758)	Linyphiidae	Generalist	*	2.75	Web building
Hahnia helveola Simon, 1875	Hahniidae	Forest species	*	2.45	Web building
Hahnia nava (Blackwall, 1841)	Hahniidae	Open-land species	*	1.75	Web building
Hahnia pusilla C.L. Koch, 1841	Hahniidae	Generalist	*	1.40	Web building
Haplodrassus silvestris (Blackwall, 1833)	Gnaphosidae	Forest species	*	7.53	Hunting
Harpactea hombergi (Scopoli, 1763)	Dysderidae	Generalist	*	5.00	Hunting
Harpactea lepida (C.L. Koch, 1838)	Dysderidae	Forest species	*	6.00	Hunting
Histopona torpida (C.L. Koch, 1837)	Agelenidae	Forest species	*	5.67	Web building
Inermocoelotes inermis (L. Koch, 1855)	Agelenidae	Forest species	*	9.64	Web building
Lathys humilis (Blackwall, 1855)	Dictynidae	Generalist	*	2.13	Web building
Linyphia hortensis Sundevall, 1830	Linyphiidae	Forest species	*	4.72	Web building
Linyphia triangularis (Clerck, 1757)	Linyphiidae	Generalist	*	6.00	Web building
Macrargus rufus (Wider, 1834)	Linyphiidae	Forest species	*	4.50	Web building

Species	**Family**	**Habitat specificity**[1, 2]	**Red List**[3]	**Mean body size (mm)**[2]	**Hunting mode**[4, 5]
Maso sundevalli (Westring, 1851)	Linyphiidae	Generalist	*	1.52	Web building
Mermessus trilobatus (Emerton, 1882)	Linyphiidae	Generalist	–	1.85	Web building
Metellina merianae (Scopoli, 1763)	Tetragnathidae	Generalist	*	9.65	Web building
Metellina segmentata (Clerck, 1757)	Tetragnathidae	Generalist	*	7.25	Web building
Micaria pulicaria (Sundevall, 1831)	Gnaphosidae	Open-land species	*	3.50	Hunting
Micrargus herbigradus (Blackwall, 1854)	Linyphiidae	Generalist	*	2.08	Web building
Micrargus subaequalis (Westring, 1851)	Linyphiidae	Open-land species	*	1.80	Web building
Microneta viaria (Blackwall, 1841)	Linyphiidae	Forest species	*	2.25	Web building
Monocephalus fuscipes (Blackwall, 1836)	Linyphiidae	Forest species	*	2.21	Web building
Neottiura bimaculata (Linnaeus, 1767)	Theridiidae	Generalist	*	2.60	Web building
Neriene clathrata (Sundevall, 1830)	Linyphiidae	Generalist	*	4.21	Web building
Neriene emphana (Walckenaer, 1841)	Linyphiidae	Forest species	*	3.80	Web building
Neriene peltata (Wider, 1834)	Linyphiidae	Forest species	*	5.25	Web building
Oedothorax apicatus (Blackwall, 1850)	Linyphiidae	Open-land species	*	2.89	Web building
Oedothorax fuscus (Blackwall, 1834)	Linyphiidae	Open-land species	*	2.15	Web building
Ozyptila praticola (C.L. Koch, 1837)	Thomisidae	Generalist	*	2.91	Hunting
Ozyptila simplex (O.P.-Cambridge, 1862)	Thomisidae	Open-land species	*	4.55	Hunting
Pachygnatha degeeri Sundevall, 1830	Tetragnathidae	Open-land species	*	3.56	Hunting
Paidiscura pallens (Blackwall, 1834)	Theridiidae	Forest species	*	1.85	Web building
Palliduphantes pallidus (O.P.-Cambridge, 1871)	Linyphiidae	Forest species	*	1.95	Web building
Panamomops mengei Simon, 1926	Linyphiidae	Forest species	D	1.50	Web building
Parasteatoda simulans (Thorell, 1875)	Theridiidae	Forest species	*	4.20	Web building
Parasteatoda tepidariorum (C.L. Koch, 1841)	Theridiidae	Generalist	*	5.50	Web building

Species	**Family**	**Habitat specificity**[1, 2]	**Red List**[3]	**Mean body size (mm)**[2]	**Hunting mode**[4, 5]
Pardosa amentata (Clerck, 1757)	Lycosidae	Generalist	*	6.00	Hunting
Pardosa hortensis (Thorell, 1872)	Lycosidae	Generalist	*	4.65	Hunting
Pardosa pullata (Clerck, 1757)	Lycosidae	Open-land species	*	4.50	Hunting
Pardosa saltans Töpfer-Hofmann, 2000	Lycosidae	Forest species	*	5.51	Hunting
Philodromus albidus Kulczyński, 1911	Philodromidae	Forest species	*	3.48	Hunting
Philodromus aureolus (Clerck, 1757)	Philodromidae	Generalist	*	5.00	Hunting
Pholcomma gibbum (Westring, 1851)	Theridiidae	Generalist	*	1.66	Web building
Phrurolithus festivus (C.L. Koch, 1835)	Phrurolithidae	Generalist	*	2.68	Hunting
Piratula hygrophila (Thorell, 1872)	Lycosidae	Generalist	*	5.31	Hunting
Piratula latitans (Blackwall, 1841)	Lycosidae	Open-land species	*	3.50	Hunting
Piratula uliginosa (Thorell, 1856)	Lycosidae	Open-land species	*	4.50	Hunting
Pocadicnemis pumila (Blackwall, 1841)	Linyphiidae	Generalist	*	1.90	Web building
Porrhomma microphthalmum (O.P.-Cambridge, 1871)	Linyphiidae	Open-land species	*	1.85	Web building
Saaristoa abnormis (Blackwall, 1841)	Linyphiidae	Generalist	*	3.41	Web building
Scotina celans (Blackwall, 1841)	Liocranidae	Generalist	V	3.09	Hunting
Tapinocyba insecta (L. Koch, 1869)	Linyphiidae	Forest species	*	1.65	Web building
Tegenaria silvestris L. Koch, 1872	Agelenidae	Generalist	*	5.50	Web building
Tenuiphantes flavipes (Blackwall, 1854)	Linyphiidae	Forest species	*	2.15	Web building
Tenuiphantes tenuis (Blackwall, 1852)	Linyphiidae	Generalist	*	2.94	Web building
Tenuiphantes zimmermanni (Bertkau, 1890)	Linyphiidae	Generalist	*	2.56	Web building
Tetragnatha nigrita Lendl, 1886	Tetragnathidae	Generalist	*	7.00	Web building
Tetragnatha obtusa C.L. Koch, 1837	Tetragnathidae	Generalist	*	6.10	Web building
Textrix denticulata (Olivier, 1789)	Agelenidae	Generalist	*	7.43	Web building

Species	Family	Habitat specificity[1, 2]	Red List[3]	Mean body size (mm)[2]	Hunting mode[4, 5]
Theridion pinastri L. Koch, 1872	Theridiidae	Generalist	*	3.50	Web building
Tiso vagans (Blackwall, 1834)	Linyphiidae	Generalist	*	2.03	Web building
Trachyzelotes pedestris (C.L. Koch, 1837)	Gnaphosidae	Open-land species	*	6.50	Hunting
Trochosa ruricola (De Geer, 1778)	Lycosidae	Open-land species	*	8.94	Hunting
Trochosa terricola Thorell, 1856	Lycosidae	Generalist	*	8.42	Hunting
Walckenaeria acuminata Blackwall, 1833	Linyphiidae	Generalist	*	3.75	Web building
Walckenaeria alticeps (Denis, 1952)	Linyphiidae	Forest species	V	2.35	Web building
Walckenaeria atrotibialis (O.P.-Cambridge, 1878)	Linyphiidae	Generalist	*	2.30	Web building
Walckenaeria corniculans (O.P.-Cambridge, 1875)	Linyphiidae	Forest species	*	2.68	Web building
Walckenaeria cucullata (C.L. Koch, 1836)	Linyphiidae	Forest species	*	2.10	Web building
Walckenaeria dysderoides (Wider, 1834)	Linyphiidae	Generalist	*	1.95	Web building
Walckenaeria incisa (O.P.-Cambridge, 1871)	Linyphiidae	Forest species	D	2.45	Web building
Walckenaeria nudipalpis (Westring, 1851)	Linyphiidae	Generalist	*	3.20	Web building
Walckenaeria vigilax (Blackwall, 1853)	Linyphiidae	Open-land species	*	2.10	Web building
Zelotes apricorum (L. Koch, 1876)	Gnaphosidae	Generalist	*	6.84	Hunting
Zilla diodia (Walckenaer, 1802)	Araneidae	Forest species	*	4.30	Web building
Zodarion italicum (Canestrini, 1868)	Zodariidae	Open-land species	*	2.58	Hunting
Zodarion rubidum Simon, 1914	Zodariidae	Open-land species	*	3.60	Hunting

[1] Hänggi, A. et al. 1995. Lebensräume Mitteleuropäischer Spinnen. – Miscellanea Faunistica Helvetiae 4, Centre de cartographie de la faune (CSCF).

[2] Nentwig, W. et al. 2017. Spiders of Europe. – <www.araneae.unibe.ch> version 07.2017.

[3] There does not exist a Red List of Switzerland. Therefore, the Red List of Baden-Württemberg is shown instead: Nährig, D. and Harms, K. H. 2003. Rote Liste und Checkliste der Spinnentiere (Arachnida) Baden-Württembergs. – Naturschutz-Praxis, Artenschutz. Threat categories are: * = least concern, D = data deficient, V = near threatened

[4] Wiki der Arachnologischen Gesellschaft e.V., ‘Hauptseite’, <https://wiki.arages.de/index.php?title=Hauptseite&oldid=91730> accessed 23 May 2017.

[5] Hunting including active hunting and ambushing

[6] Bell, J. R. et al. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. – B. Entomol. Res. 95: 69–114.

S4 Table. Correlations within and among landscape and site characteristics. Results of Pearson’s (r) and Spearman’s rank (r_s) correlation, Contingency table (χ^2-test) and Kruskal-Wallis test examining the relationship between observed species richness and rarefied species richness (a) and among landscape and forest characteristics for all three taxonomic groups (b), in the vegetation plots (c) and in the trap-grid system (d).

a) Species richness and functional richness

Observed species richness vs. sample-based rarefied species richness		
Ants	Pearson	**r = 1.00, n = 26, P < 0.001**
Spiders	Pearson	**r = 1.00, n = 26, P < 0.001**

b) Variables considered in all three taxonomic groups

Landscape characteristics Percentage cover of …		
Radius = 200 m		
Sealed area vs. forest cover	Spearman	**r_s = –0.47, n = 26, P = 0.015**
Sealed area vs. agricultural land	Spearman	**r_s = –0.54, n = 26, P = 0.005**
Sealed area vs. urban green space	Spearman	**r_s = 0.65, n = 26, P < 0.001**
Radius = 500 m		
Sealed area vs. forest cover	Spearman	**r_s = –0.66, n = 26, P < 0.001**
Sealed area vs. agricultural land	Spearman	**r_s =–0.57, n = 26, P = 0.002**
Sealed area vs. urban green space	Spearman	**r_s =0.52, n = 26, P = 0.007**
Sealed area: R = 200 m vs. R = 500 m	Pearson	**r = 0.88, n = 26, P < 0.001**

Shape index		
Degree of urbanisation vs. shape index	χ^2-test	χ^2 = 3.87, df = 4, P = 0.42
Forest size vs. shape index	χ^2-test	χ^2 = 8.06, df = 4, P = 0.089

Historical development		
Degree of urbanisation vs. history	χ^2-test	χ^2 = 6.09, df = 4, P = 0.19
Forest size vs. history	χ^2-test	**χ^2 = 12.97, df = 4, P = 0.011**

Recreational pressure		
Path density vs. total trampled area	Spearman	**r_s = 0.52, n = 26, P = 0.007**

c) Variables considered in vegetation plots

Species richness vs. cover of ground vegetation	Spearman	r_s = 0.19, n = 26, P = 0.36

Soil and litter characteristics		
Soil organic matter content vs. Soil organic nitrogen content	Spearman	**r_s = 0.85, n = 26, P < 0.001**

d) Variables considered in trap-grid system

Soil and litter characteristics		
Soil moisture vs. ln(soil organic matter content)	Pearson	**r = 0.40, n = 26, P = 0.044**
Soil pH vs. ln(soil organic matter content)	Spearman	**r_s = 0.57, n = 26, P = 0.002**
Soil moisture vs. litter moisture	Pearson	**r = 0.52, n = 26, P = 0.006**
Soil pH vs. litter pH	Spearman	**r_s = 0.56, n = 26, P = 0.003**

S5 Table. Species–site matrices for plants, ants, and spiders. For the arthropod survey, the number of recollected traps per forest site is presented.
https://doi.org/10.1371/journal.pone.0199245.s006

S6 Table. Data used to perform PERMANOVA.
https://doi.org/10.1371/journal.pone.0199245.s007

S7 Table. Percentage of sites in which common species occur for different degrees of urbanisation and forest size classes. Common species are defined as occurring in at least 10 of the sites. Means are given for less common species.
https://doi.org/10.1371/journal.pone.0199245.s008

S8 Table. Functional dispersion: Summary of ANCOVAs of plants. Summary of ANCOVAs examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil characteristics (moisture, pH, soil organic nitrogen (orgN) and phosphorus (orgP) content) and cover of ground vegetation on functional dispersion of vascular plants.

	Functional dispersion		
	df	F	P
Degree of urbanisation	2,16	3.92	**0.041**
Forest size	2,16	3.68	**0.049**
Shape index	2,16	1.67	0.34
Time since last thinning	2,16	4.94	**0.021**
Path density	–	–	–
Canopy closure	–	–	–
Soil moisture content	–	–	–
Soil pH	–	–	–
Soil organic nitrogen content[1]	–	–	–
Soil organic phosphorus content[1]	1,16	1.56	0.23
Cover of ground vegetation	–	–	–
Degree of urbanisation*forest size	–	–	–

Significant P-values (< 0.05) are in bold

[1] log-transformed

– Factor was excluded from the model by step-wise reduction

S9 Table. Functional dispersion: Summary of ANCOVAs of ants and spiders. Summary of ANCOVAs examining the effects of degree of urbanisation, forest size and shape, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, soil organic matter content, litter characteristics (moisture, pH) and structural diversity measures (litter biomass, vegetation structure and amount of dead wood) on functional dispersion of ants and spiders.

	Functional dispersion		
	df	F	P
Ants			
Degree of urbanisation	2,13	1.82	0.20
Forest size	2,13	3.68	0.054
Shape index	–	–	–
Time since last thinning	–	–	–
Path density	–	–	–
Canopy closure	1,13	3.19	0.097
Soil organic matter content[1]	1,13	0.18	0.68
Litter moisture content	1,13	12.63	**0.004**
Litter pH	1,13	3.29	0.093
Amount of litter biomass[1]	–	–	–
Vegetation structure[1]	–	–	–
Amount of dead wood	–	–	–
Degree of urbanisation*forest size	4,13	2.76	0.074
Spiders			
Degree of urbanisation	2,20	1.91	0.17
Forest size	2,20	2.86	0.081
Shape index	–	–	–
Time since last thinning	–	–	–
Path density	–	–	–
Canopy closure	–	–	–
Soil organic matter content[1]	–	–	–
Litter moisture content	–	–	–
Litter pH	–	–	–
Amount of litter biomass[1]	–	–	–
Vegetation structure[1]	1,20	1.33	0.26
Amount of dead wood	–	–	–
Degree of urbanisation*forest size	–	–	–

Significant P-values (<0.05) are in bold

[1] log-transformed

– Factor was excluded from the model by step-wise reduction

Chapter III

Ecosystem functioning in cities: Combined effects of urbanisation and forest size on early-stage leaf litter decomposition of European beech (*Fagus sylvatica* L.)

Ramona L. Melliger, Hans-Peter Rusterholz, Bruno Baur

Urban Forestry & Urban Greening, 2017, **28**: 88–96

Urban Forestry & Urban Greening 28 (2017) 88–96

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

journal homepage: www.elsevier.com/locate/ufug

Original article

Ecosystem functioning in cities: Combined effects of urbanisation and forest size on early-stage leaf litter decomposition of European beech (*Fagus sylvatica* L.)

Ramona Laila Melliger*, Hans-Peter Rusterholz, Bruno Baur

Section of Conservation Biology, Department of Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland

ARTICLE INFO

Keywords:
Decomposition rate
Forest area
Leaf chemical characteristics
Microbial activity
Plant diversity
Temperate deciduous forests

ABSTRACT

Environmental changes associated with urbanisation can affect the functioning of ecosystem processes. In cities, forests are among the most frequent types of green areas and provide a wide range of ecosystem services including air cleaning, decomposition of leaf litter and recreation. The European beech (*Fagus sylvatica*) is a frequent and widespread deciduous tree in temperate forests in Central Europe. In this study, we examined the effects of urbanisation on decomposition processes of *F. sylvatica* leaves in different-sized forests in the urban region of Basel, Switzerland. We used standardised litterbags (mesh size: 2 mm) with *F. sylvatica* leaves to assess the impact of degree of urbanisation (indicated by the percentage cover of sealed area in the surroundings) and forest size on the early stage of leaf litter decomposition and seasonal microbial activity. We found combined effects of degree of urbanisation and forest size on the decomposition rate of leaf litter (k_{litter}). Large forests showed the highest k_{litter} in areas with sparse settlements and the lowest k_{litter} in densely settled areas, whereas the opposite pattern was recorded for small and medium-sized forests. This indicates that abiotic and biotic forest characteristics of forests of similar size differently influenced k_{litter} depending on the degree of urbanisation. Moisture content of litter was the best predictor of microbial activity, followed by forest size. We assume that factors acting at the landscape scale such as the degree of urbanisation might be too coarse to detect any differences in microbial activity. Our results revealed that even small urban forests contribute to this important ecosystem function. As decomposers are at the bottom of the food chain, management actions that support the biological activity in soil might be also beneficial for species at higher trophic ranks.

1. Introduction

Urban growth is considered to be a major driver of environmental change (Grimm et al., 2008). Urbanisation-related factors including reduced habitat size and increased spatial isolation change the dynamics of plant and animal populations in the remaining green areas (Niemelä, 1999; McKinney, 2002; Melliger et al., 2017). Furthermore, environmental conditions in the remaining habitat patches are affected. Studies along urbanisation gradients showed increases in temperature, precipitation and N deposition from the rural surroundings to the city centre (Grimm et al., 2008; Pickett et al., 2011). These changes influence habitat quality and subsequently plant species richness and composition (Sukopp, 1998; Gehlhausen et al., 2000; Vallet et al., 2010), which in turn affect the functioning of ecosystems (Chapin et al., 1997; Hooper and Vitousek, 1997; McDonnell et al., 1997).

Forests are among the most frequent types of green areas in cities and provide a wide range of ecosystem functions, from habitat for native species to the recycling and storage of nutrients, air filtering, temperature regulation and recreation to residents (Dwyer et al., 1992; Bolund and Hunhammer, 1999; Berg and McClaugherty, 2014). The decomposition of leaf litter is an important ecosystem function in forests (McDonnell et al., 1997). It mineralises nutrients into forms accessible for plants and thus is a key component of the process of nutrient cycling and the formation of soil (Swift et al., 1979; Berg and McClaugherty, 2014). The decomposition rate depends on various factors including the physical and chemical characteristics of leaf litter, climatic conditions (e.g. temperature, precipitation), the composition and feeding activity of decomposers and local soil characteristics (e.g. soil moisture, pH and soil nutrients; Swift et al., 1979; Nikula et al., 2010; McClaugherty and Berg, 2011). Urbanisation alters some of these factors and thus may influence the decomposition rate of leaf litter and chemical leaf litter characteristics (e.g. lignin, nitrogen, phosphorus) in different ways (Pouyat and Carreiro, 2003; Pavao-Zuckerman and Coleman, 2005). For example, edge effects such as increased

---

* Corresponding author.
E-mail addresses: ramona.melliger@unibas.ch (R.L. Melliger), hans-peter.rusterholz@unibas.ch (H.-P. Rusterholz), bruno.baur@unibas.ch (B. Baur).

http://dx.doi.org/10.1016/j.ufug.2017.10.009
Received 9 February 2017; Received in revised form 5 October 2017; Accepted 12 October 2017

temperature, solar radiation and moisture stress are pronounced in urban forest fragments due to huge differences between matrix and forests (Hamberg et al., 2009 and references therein). These effects are further enhanced in small forests, which contain higher proportions of edge habitat than large forests (Matlack, 1993; Gehlhausen et al., 2000). However, the effect of forest size on leaf litter decomposition in urban areas has, so far, not been examined.

In temperate forests, microorganisms, encompassing both fungi and bacteria, represent the dominant primary decomposers and play a key role in the early stage of leaf decomposition. In particular, the enzymatic activity of microorganisms increases the palatability of litter debris for soil animals by degrading polymer structures like lignin, cellulose and hemicellulose into smaller and more easily digestible molecules (Berg and McClaugherty, 2014). Therefore, changes in the soil microbial activity can have severe consequences on the decomposition rate of leaf litter in forest ecosystems.

The few studies assessing general effects of urbanisation on leaf litter decomposition in forests yielded contrasting results. Compared with rural forests, decomposition rates of leaf litter in urban forests were either higher (McDonnell et al., 1997; Pouyat et al., 1997; Pouyat and Carreiro, 2003; Nikula et al., 2010), lower (Pavao-Zuckerman and Coleman, 2005) or showed no difference (Enloe et al., 2015). Most of these studies were conducted in forests in North America using litterbags with leaves of *Quercus* sp. (e.g. Pouyat and Carreiro, 2003; Pavao-Zuckerman and Coleman, 2005). In Europe, urban studies on leaf decomposition are restricted to *Q. ilex* in Mediterranean forests (Cotrufo et al., 1995) and *Populus tremula* in boreal forests (Nikula et al., 2010). By using microcosms, Cotrufo et al. (1995) recorded lower decomposition rates for leaf litter sampled in the city than for leaf litter collected outside the city in the early stage of decomposition. In contrast, Nikula et al. (2010) reported a faster decay of leaf litter at urban sites and for urban litter after 13 months of incubation.

The European beech (*Fagus sylvatica* L.) is one of the most frequent deciduous tree species in temperate forests in Central Europe (Bolte et al., 2007). Several studies compared the decomposition rate of *F. sylvatica* leaves with those of other tree species and leaf litter mixtures in rural landscapes (Anderson, 1973; Jacob et al., 2010). *F. sylvatica* leaves show the highest C/N-ratio and lignin concentrations and thus decompose more slowly than leaves of the other tree species investigated. So far, however, effects of urbanisation on the decomposition process of *F. sylvatica* leaves have not been examined.

In this study, we used standardised litterbags with leaves of *F. sylvatica* to assess the impact of urbanisation-related factors on the early stage of decomposition and seasonal microbial activity. Litterbags were exposed in temperate deciduous forests of different size in the city of Basel (Switzerland) and its suburban surroundings for periods of different lengths. In particular, we examined the potential influence of degree of urbanisation and forest size on the decomposition rate. We expected that decomposition rate of leaf litter (k_{litter}) increases with the degree of urbanisation, because higher temperatures in highly urbanised areas compared to less urbanised areas have been reported to stimulate decomposer activity (Pouyat et al., 1997; Pouyat and Carreiro, 2003). As smaller forests are assumed to contain a higher proportion of edge habitat with increased moisture stress compared to larger forests (Matlack, 1993; Gehlhausen et al., 2000), we also expected an increase in decomposition rate with urban forest size. Similarly to k_{litter}, we expected the decomposition rate of lignin − a key factor of litter breakdown – to increase with degree of urbanisation and forest size. However, the effect will be less pronounced due to the low decomposability of lignin.

Finally, we examined which factors (degree of urbanisation, forest size, litter moisture, plant species richness and others) determine microbial activity in leaf litter of urban forests at different sampling dates.

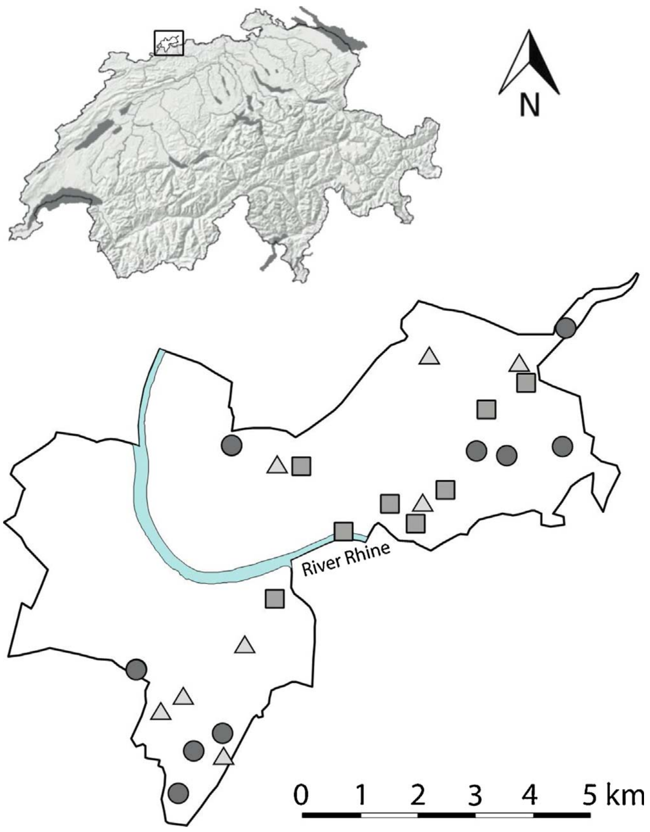


Fig. 1. Location of the study area in Northwestern Switzerland and the distribution of the forest sites examined in the area of Basel-Stadt. Forests were grouped according to their size in three classes: small (triangle), medium-sized (rectangle) and large (circle) forests. The investigation area is surrounded by dense settlements in Germany (north), France (northwest) and Switzerland (south-west).

2. Methods

2.1. Study area

The study was conducted in Basel-Stadt (comprising the city of Basel and the municipalities Riehen and Bettingen; hereafter referred to as Basel, Fig. 1), Switzerland (47°34′N, 7°36′E, elevation: 245–522 m a.s.l.). The study area covers 37 km^2, consisting of 26.2 km^2 (70.9%) residential area, 4.5 km^2 (12.1%) agricultural land, 4.4 km^2 (11.7%) forest and 1.7 km^2 (4.5%) water bodies (Statistisches Amt Kanton Basel-Stadt: www.statistik-bs.ch, 2015). Basel has 196′471 inhabitants and a population density of 5320 inhabitants km^{-2} (www.statistik-bs.ch, 2015). Total annual precipitation averages 842 mm and annual mean temperature is 10.5 °C (records from 1982 to 2010; MeteoSwiss, 2015).

2.2. Forest characteristics and vegetation survey

To investigate the potential effects of degree of urbanisation and forest size on leaf litter decomposition, we chose 25 deciduous forest sites, belonging to the Fagetum association (Burnand and Hasspacher, 1999) and ranging in size from 258 m^2 to 50,000 m^2 (Fig. 1; Table S1). The forest sites examined differ in their historical development and consequently in age. Nineteen of them are surrounded by settlements and agricultural lands and are no longer connected to large continuous forests ($>$ 40 ha; see Table S1 for detailed description of forests). These forest sites are either remnants of former large continuous forests (fragments) or a result of abandonment of orchards or planted after 1884 (planted).

In each forest site, three randomly chosen sampling plots measuring 4 m × 4 m were installed. Species richness of vascular plants in the

Table 1
Chemical composition of initial leaf litter of *F. sylvatica* (mean ± SE; N = 60 in each case).

	Initial litter (mean ± SE)
Lignin (%)	20.04 ± 0.47
C (%)	44.45 ± 0.04
N (%)	0.967 ± 0.004
C:N	45.88 ± 0.24
P (μg g^{-1})	1015.31 ± 14.87

ground vegetation (< 40 cm) was assessed for each plot and the total cover of ground vegetation was estimated using the Braun-Blanquet scale (Braun-Blanquet, 1964). Canopy closure was assessed based on three photographs in each plot and determined with the pixel counting function of Adobe Photoshop (version 10.0.1). Plant surveys were carried out once in spring and once in autumn 2013.

2.3. Litter preparation and sampling

Leaf litter decomposition rates were quantified using litterbags with standardised beech (*Fagus sylvatica*) litter. Recently fallen senescent leaves of *F. sylvatica* were collected in a forest 5 km southwest of Basel in October and November 2014 and dried at 50 °C for 48 h 4.0 g of dried leaves were filled in nylon litterbags (12 cm × 15 cm) with a mesh size of 2 mm × 2 mm, which allowed access of the soil micro- and mesofauna to the leaf litter (Swift et al., 1979). To characterise the initial leaf litter, a subsample was ground and the ash-free dry mass (AFDM in %) and concentrations of carbon, nitrogen, phosphorus and lignin were assessed (see below; Table 1).

In January 2015, nine litterbags were placed on the soil surface in each of the three plots (27 litterbags per forest site, 675 in total) and covered with leaf litter. The litterbags were placed in a small homogeneous area (1 m × 1 m) of each plot to minimise potential effects of different soil and microclimatic conditions. Three litterbags were collected from each plot in March (after 2 months), three in May (after 4 months) and three in September 2015 (after 8 months). In case of missing litterbags, only one or two bags were collected on the sampling date concerned. The remaining litter of the bags was weighed and a subsample was stored at 4 °C to assess microbial activity (FDA; see below). The rest of the litter was dried (50 °C for 48 h), weighed and ground. Moisture content of litter (%) was determined using the fresh to dry weight ratio of leaves.

To characterise the microclimatic conditions of the soil surface, data loggers (Tinytag Talk 2–Gemini TK-0014 Data Logger, Chichester, West Sussex) were buried at a depth of 2 cm in one plot in each of nine forest sites. To avoid soil disturbance around the litterbags, data loggers were buried at a distance of 50 cm to them. Temperature was recorded hourly between mid-March and early October 2015.

2.4. Nutrient concentrations and microbial activity of litter

Subsamples of the initial litter and of litter from bags resampled at each date were ashed at 500 °C for 4 h to determine AFDM. To assess the concentration of the nutrients in a plot, the leaf litter of the three bags per plot was pooled for each sampling date. Percentage of carbon and nitrogen were determined with a CN analyser (LECO CHN628 Series Elemental Analyser, St. Joseph, Michigan). Total organic phosphorus content (μg $PO_4^{3-}g^{-1}$) was determined using the molybdenum blue method (Sparks et al., 1996). Lignin concentration was assessed with protein-free litter using the acetyl bromide method (Moreira-Vilar et al., 2014). Because soil contamination was evident in several litterbags, oven-dry litter masses and concentrations of nitrogen, phosphorus and lignin were corrected for following Blair (1988).

Fluorescein diacetate (FDA) hydrolysis is a surrogate for microbial activity (comprising bacteria and fungi; Schnürer and Rosswall, 1982). We assessed the effect of urbanisation degree and forest size on the hydrolyse activity of FDA by using a slightly modified method of Dick et al. (1996). Approximately 0.1–0.2 g of field-moist leaf litter was cut in small pieces, mixed with 10 ml of sodium phosphate buffer (6.0 mM, pH 7.6) and homogenised for 1 min with a Brinkmann Polytron (Kinematica, Luzern). To start the reaction, 100 μl FDA (4.8 mM) was added. After an incubation time of 30 min at 37 °C, 10 ml of acetone:-water (1:1) was added to stop the reaction. The litter suspensions were centrifuged for 5 min at 4000 rpm and the absorbance was measured spectrophotometrically at 490 nm.

2.5. Soil characteristics

To examine any potential influences of soil characteristics on decomposition rate, three soil samples per plot were collected 20 cm from the litterbags using a metal cylinder (depth: 5 cm; diameter 5.05 cm; volume 100 cm^3) on each sampling date (March, May, September 2015). The three soil samples of a plot were pooled, mixed and transported to the laboratory, where they were sieved (mesh size 2 mm) and dried at 50 °C for 48 h. Soil moisture content (%) was determined using the fresh to dry weight ratio and soil pH was assessed in distilled water (1:2.5 soil:water; Allen, 1989). Total soil organic matter content was determined as loss-on-ignition of oven dried soil at 750 °C for 16 h (Allen, 1989). Total organic nitrogen content was assessed using the standard method of Kjeldahl (Bremner, 1965). To assess total organic phosphorus content of the soil, the same method as described for leaf litter was applied.

2.6. Degree of urbanisation and recreational pressure

The forests examined in our study are very small and embedded in a small-scattered landscape, where settlements and green areas are located within short distances. An urban–rural gradient approach extending over several kilometres is not appropriate. Therefore, we used the percentage cover of sealed area (built-up area and traffic infrastructure) in the closer surroundings of the forest sites as a measure of degree of urbanisation, as suggested by others (e.g. McDonnell and Hahs, 2008; Vallet et al., 2010).

Land cover data were derived from satellite images (Google Earth, 2009, date: 6 May 2014). Around the most central sampling plot in each forest site, the percentage cover of sealed area was determined within radii of 200 m and 500 m using the pixel counting function of Adobe Photoshop (version 10.0.1).

Two different measures were applied to estimate the impact of recreational pressure on litter decomposition: (1) path density expressed as the total path length per forest site (in m/ha), and (2) the total trampled area within a forest site (expressed in % of forest area).

2.7. Data analyses

All statistical analyses were performed using the software R (R Development Core Team, 2013, version 3.0.2). Since percentage sealed area within the two radii were positively correlated (Spearman rank correlation, $r_s = 0.82$, $N = 25$, $P < 0.001$), only data within the 500-m radius were considered in subsequent analyses. In a first step, degree of urbanisation and forest size were used either as continuous variables or as factors to examine their potential effects on decomposition rate and microbial activity. However, because the two approaches revealed very similar results, only the results of the second approach are presented. Based on the percentage cover of sealed area in their surroundings, the forest sites were classified into areas with low (< 15%), medium (15–30%) or high (> 30%) degree of urbanisation. Forest sites were also divided into three size classes: small (< 4000 m^2), medium-sized (4000–10,000 m^2) or large (> 10,000 m^2) forests (Fig. 1; Table S1). The historical development of forests (forest history: continuous, fragmented, planted forests; Table S1) was confounded with both the degree of urbanisation and forest size (Kruskal-Wallis, forest history vs. degree of urbanisation: $\chi^2 = 6.71$, $df = 2$, $P = 0.035$; forest history vs. forest size: $\chi^2 = 12.60$, $df = 2$, $P = 0.002$) and thus excluded from the subsequent analyses.

Two-way analyses of variance (ANOVA) or Kruskal-Wallis tests were applied to assess whether mean species richness and cover of ground vegetation and soil characteristics per sampling plot differed between the three classes of degree of urbanisation and forest size, respectively. Preliminary analyses revealed inter-correlations among soil variables (soil moisture vs. total organic nitrogen content: $r_s = 0.39$, $N = 25$, $P = 0.055$; soil pH vs. total soil organic matter: $r_s = 0.49$, $N = 25$, $P = 0.014$; soil pH vs. total organic phosphorus content: $r_s = 0.59$, $N = 25$, $P = 0.002$). Therefore, total soil organic matter content, total soil organic nitrogen and phosphorus content were excluded from the subsequent analyses. Multiple comparisons (post hoc tests) were performed to compare differences among the classes of degree of urbanisation and forest size, using the *TukeyHSD* function in the stats package for ANOVAs and the *posthoc.kruskal.nemenyi.test* function in the *PMCMR* package for Kruskal-Wallis tests in R.

Because mass losses of leaf litter, lignin and carbon were linear in the 8-month period of incubation, we applied linear regressions instead of negative exponential curves to calculate mean daily decomposition rate constants (k_{litter}, k_{lignin} and k_{carbon}) during this early stage of decomposition (Wieder and Lang, 1982; Xuluc-Tolosa et al., 2003; Jacob et al., 2010):

$$X_t = -k^* t + X_0$$

where X_t is the remaining mass (g) at time t (days), X_0 the initial leaf mass and k is the decomposition rate constant (mg g^{-1} d^{-1}). However, as k_{lingin} and k_{carbon} were positively correlated ($r_s = 0.33$, $N = 25$, $P = 0.005$) and showed similar results, we only present the results for k_{lignin}. The mass losses of nitrogen and phosphorus showed neither a linear nor negative exponential decay curve. Hence, decomposition rates could not be calculated for these two leaf litter characteristics.

Linear mixed-effects models (LME) for pseudo-replicated data were used to examine the effects of degree of urbanisation and forest size on the decomposition rate of leaf litter (k_{litter}) and lignin (k_{lignin}). The models were structured as nested randomised block designs, with degree of urbanisation and forest size and the corresponding interaction as fixed factors and sampling plot nested in forest as random factor. Management of forest sites ('time since last thinning': < 3 years, 4–10 years or > 10 years ago) were used as factors and path density, canopy closure, soil moisture content, soil pH and species richness of ground vegetation as cofactors. For the second and third sampling period, we used mean values of soil moisture content and soil pH including the previous sampling dates. Due to inter-correlations between the two measures of recreational pressure (path density vs. total trampled area: $r_s = 0.43$, $N = 25$, $P = 0.033$) and between canopy closure and cover of ground vegetation ($r_s = -0.33$, $N = 25$, $P = 0.005$), total trampled area and cover of ground vegetation were not considered in the subsequent analyses. Microbial activity was not included in these LME models, because it was determined at single time points and thus was not suitable as potential factor influencing the decomposition processes over several months. All models were stepwise reduced as recommended by Crawley (2007). Multiple comparisons (Tukey Contrasts) were performed to compare differences among degree of urbanisation, forest size and time since last thinning, respectively, using the *glht* function in the *multcomp* package in R.

The same LMEs with stepwise reduction were used to examine the impacts of degree of urbanisation and forest size on the hydrolyse activity of FDA (hereafter referred to as 'microbial activity') at the three sampling dates: early spring, late spring and autumn. As microbial activity is determined by environmental conditions on a small spatial scale, we used leaf litter moisture instead of soil moisture content as a cofactor in the LME models. Both variables were positively inter-correlated (all sampling periods, $r > 0.27$, $N = 25$, $P < 0.05$). Furthermore, total soil organic nitrogen content was included as a cofactor. From the 675 litterbags exposed, 647 litterbags (95.9%) could be retrieved. The missing bags were concentrated in a few plots, which were excluded from analyses (two plots in May and five plots in September).

3. Results

3.1. Characteristics of forest sites

In the ground vegetation of the 25 forest sites examined, a total of 88 vascular plant species was recorded; 62 species (70.5%) were found in small, 61 species (69.3%) in medium-sized and 63 species (71.6%) in large forests (Table S2). Mean species richness per sampling plot was negatively related to the degree of urbanisation (ANOVA, $P = 0.041$; Table S3), but did not differ among forest size classes ($P = 0.75$). In contrast, total cover of ground vegetation in the plots was negatively related to forest size ($P = 0.006$), but was not affected by the degree of urbanisation ($P = 0.47$; Table S3). Forests with sparse settlement in their surroundings harboured higher species richness than forests in areas with medium or high degree of urbanisation. Concerning forest size, small and medium-sized forests showed a higher vegetation cover than large forests (Table S3).

The temperature of soil surface in the forest sites was not influenced by the degree of urbanisation (Kruskal-Wallis, $P = 0.79$; Table S4). In contrast, considering the entire measuring period, soil surface temperature in large forests was on average 1 °C colder than in small and medium-sized forests (Table S4; Fig. S1).

Soil moisture content in forest sites examined differed in relation to the degree of urbanisation (ANOVA, all sampling periods $P < 0.047$, Table S3). Forests located in areas with a medium degree of urbanisation exhibited marginally lower soil moisture content than forests in areas with a low or high degree of urbanisation (Table S3). Furthermore, in late spring, soil moisture was significantly higher in large than in medium-sized forests (Table S3). Soil pH differed among forests of different size (Kruskal-Wallis, all sampling periods $P < 0.013$). Soil pH was significantly higher in small and medium-sized forests than in large forests (Table S3). However, soil pH was not affected by the degree of urbanisation (Kruskal-Wallis, all sampling periods $P > 0.76$).

3.2. Litter mass loss and decomposition rate

The mass of *F. sylvatica* litter remaining after 8 months was highest in forest sites surrounded by dense settlement (mean ± SE: 88.7 ± 1.4%) and lowest in areas with low degree of urbanisation (86.1 ± 0.9%; Fig. 2a; Table S5). In forests situated in areas with low and medium degrees of urbanisation, leaf litter mass declined consistently during the entire sampling period (Fig. 2a). In contrast, forests surrounded by dense settlements showed two successive periods of decomposition with different rates; in the first period decomposition was relatively fast (January–March), in the second (April–September) slower (Fig. 2a). Considering forest size, remaining litter mass was highest in small (88.2 ± 1.3%) and lowest in medium-sized forest sites (85.6 ± 0.8%; Fig. 2b; Table S6). In small and large forests, the loss of leaf litter mass was faster in the first 2 months of incubation and thereafter slowed down, whereas the opposite pattern could be observed for medium-sized forests (Fig. 2b).

Considering the leaf litter characteristics examined, the percentage of initial mass of lignin and carbon constantly decreased during the sampling period (Linear regression: lignin: $R^2 = 0.62$, $df = 73$, $P < 0.001$; carbon: $R^2 = 0.73$, $df = 73$, $P < 0.001$; Table S5 and S6). The percentage of initial mass of lignin further differed among forest size classes after 8 months of incubation (ANOVA, $F_{2,22} = 3.96$, $P = 0.034$), being higher in large than medium-sized forests (Table S6).

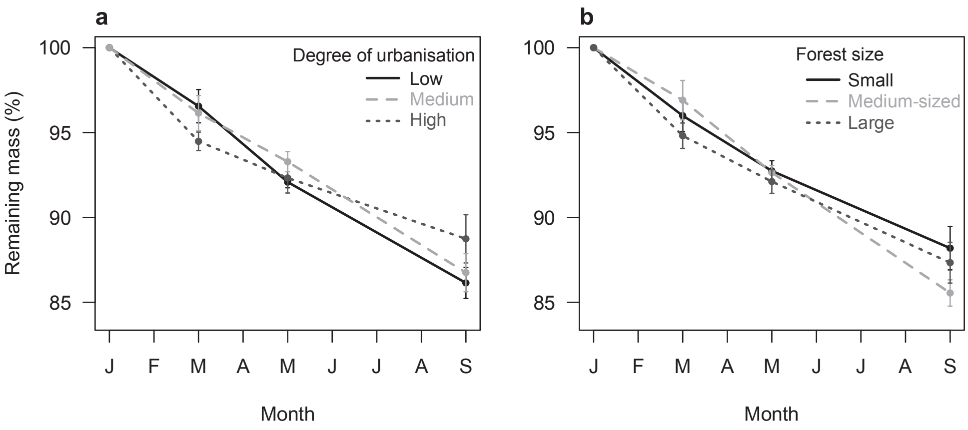


Fig. 2. The mass of initial litter remaining after 2, 4 and 8 months of incubation (mean ± SE) in forests located in areas with different degree of urbanisation (a), and in forests of different size (b).

In contrast to lignin and carbon, percentage of initial mass of nitrogen decreased in the first 2 months and that of phosphorus in the first 4 months of incubation and thereafter slightly increased again (Table S5 and S6), indicating net accumulation of nitrogen and phosphorus due to microbial immobilization (Nikula et al., 2010).

The decomposition rate of litter (k_{litter}) was positively related to forest size, being higher in large than in small and medium-sized forests (Tukey Contrasts: large vs. small: $P = 0.012$; large vs. medium-sized: $P < 0.001$) and showed a weak trend for the degree of urbanisation (Table 2; Fig. 3a, b). We also recorded a significant interaction between degree of urbanisation and forest size: large forests showed the highest k_{litter} in less urbanised areas and the lowest k_{litter} in densely populated areas, whereas the opposite pattern was observed for small and medium-sized forests (Table 2; Fig. 4). Furthermore, k_{litter} increased with soil moisture content and was affected by soil pH (Table 2; Fig. S2a, b). The decomposition rate of lignin (k_{lignin}) was neither affected by the degree of urbanisation nor by forest size (Table 2). However, k_{lignin} was positively related to soil moisture content ($F_{1,44} = 5.74$, $P = 0.021$; Table 2; Fig. S2c). Time since last thinning, path density, canopy closure and the species richness of ground vegetation had no impacts on k_{litter} *and* k_{lignin} (Table 2).

3.3. Microbial activity

Microbial activity of leaf litter expressed as the hydrolyse activity of FDA did not differ among the three classes of the degree of urbanisation at any of the three sampling dates (Table 3; Fig. S3). However, microbial activity was affected by forest size in late spring (Fig. S3a). An interaction between degree of urbanisation and forest size was observed in autumn: microbial activity in small and medium-sized forests decreased with increasing degree of urbanisation, while the microbial activity in large forest sites only marginally increased from forests with sparse to those with rather dense settlements in their surroundings (Fig. 5).

Table 2
Results of LME analyses testing the effects of the degree of urbanisation, forest size, forest management (time since last thinning), recreational pressure (indicated by path density), canopy closure, soil characteristics (moisture, pH) and species richness of ground vegetation on the decomposition rate of litter (k_{litter}) and lignin (k_{lignin}).

	k_{litter} [a]			k_{lignin}		
	df	*F*	*P*	*df*	*F*	*P*
Degree of urbanisation	2,16	2.87	0.086	2,20	1.72	0.20
Forest size	2,16	5.38	**0.016**	2,20	0.19	0.83
Time since last thinning	–	–	–	–	–	–
Path density	–	–	–	–	–	–
Canopy closure	–	–	–	–	–	–
Soil moisture	1,43	16.27	**< 0.001**	1,44	5.74	**0.021**
Soil pH	1,43	11.91	**0.001**	–	–	–
Species richness of ground vegetation [a]	–	–	–	–	–	–
Degree of urbanisation*forest size	4,16	6.21	**0.003**	–	–	–

Significant *P* values (< 0.05) are in bold.
– Factor was excluded from the model by step-wise reduction.
[a] sqrt-transformed.

Microbial activity was positively related to litter moisture content at all three sampling dates (Table 3; Fig. S3b–d). In late spring, microbial activity was also affected by the time since last thinning (Table 3; Fig. S3e). It was higher in forest sites, which were managed more than 10 years ago than in forest sites, which were thinned 4–10 years ago (Tukey Contrasts, 4–10 y vs. > 10 y: $P = 0.040$). Microbial activity was also influenced by the species richness of the ground vegetation (Fig. S3f). In autumn, microbial activity decreased with increasing path density (Table 3; Fig. S3h).

4. Discussion

Our study revealed combined effects of the degree of urbanisation and forest size on the decomposition rate of *F. sylvatica* in the early stage of decomposition. The results further indicated that moisture content of litter was the best predictor for microbial activity and that the other forest and plot characteristics examined showed different influences depending on the sampling date, which reflects both a seasonal and climatic condition and the stage of decomposition.

4.1. Soil characteristics and vegetation data

Soil moisture is a key component for soil functioning and can be modified by several biotic and abiotic factors including vegetation structure, air temperature and soil disturbance (Pickett et al., 2011). In our study, soil moisture differed among forest sites located in areas with different degree of urbanisation. However, our finding that soil moisture content of forests located in areas with dense and sparse settlements was similar and even slightly higher than that of forests located in areas with medium degree of urbanisation was rather surprising, as we expected soil moisture content to decrease with degree of urbanisation. The fact that we did not record any differences in soil temperature among the three classes of degree of urbanisation might partly explain this pattern. However, our finding might also be a result of combined effects of different designs of studies and differences in the spatial dimension of the study areas. The majority of studies, which assessed the effect of urban sprawl on biotic and abiotic characteristics of a given habitat, used urban–rural gradients with distances ranging from several kilometres up to 130 km (e.g. Pouyat et al., 1997). In contrast, the forests examined in our study were embedded in a small-scattered landscape, where settlements and green areas are located within short distances. Therefore, we used the percentage cover of

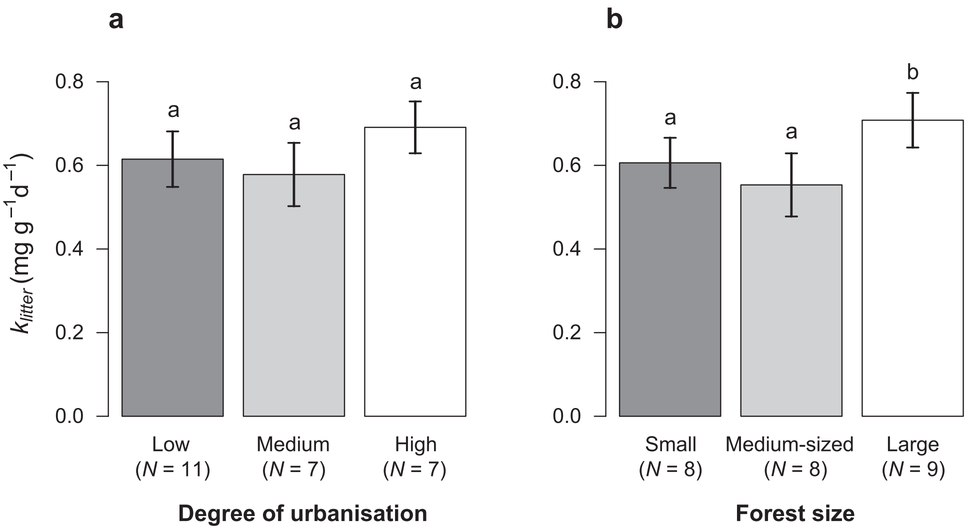


Fig. 3. Leaf litter decomposition rates (k_{litter}; mean ± SE) of *F. sylvatica* in forests located in areas with different degrees of urbanisation (a) and of different size (b). Different letters indicate significant differences among classes.

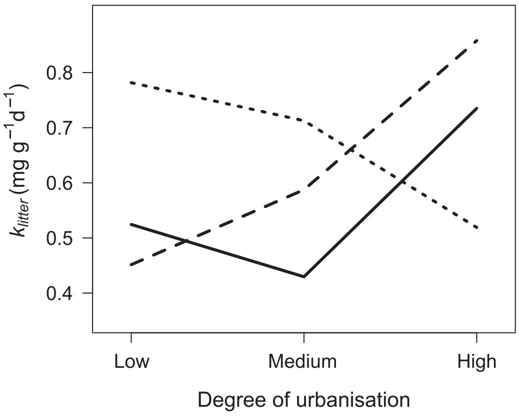


Fig. 4. Decomposition rate of litter (k_{litter}) in small (solid line), medium-sized (dashed line) and large (dotted line) forests located in areas with different degree of urbanisation.

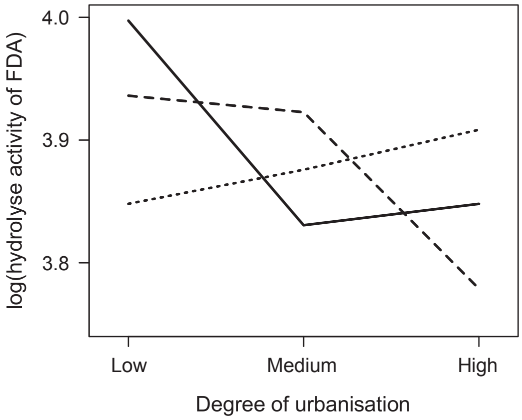


Fig. 5. Microbial activity (expressed as the hydrolyse activity of FDA) in small (solid line), medium-sized (dashed line) and large (dotted line) forests located in areas with different degree of urbanisation.

sealed area in the closer surroundings of the forests as a measure of degree of urbanisation, which allows an assessment of small-scale effects of urbanisation on soil moisture.

Beside degree of urbanisation, soil moisture content was only slightly affected by forest size in late spring. This finding could be explained by differences in vegetation cover among the three classes of forest size (Table S3). Hence, the high vegetation cover in small and medium-sized forests compared to large forests may have mitigated the expected area-related effects on soil moisture content. Another explanation for the low impact of forest size on soil moisture content is that even the large forest sites in our study were probably too small to preserve an undisturbed interior forest environment (Matlack, 1993; Gehlhausen et al., 2000).

Urban areas frequently harbour more plant species than their rural surroundings partly as a result of introduction and dispersal of non-

Table 3

Results of LME analyses testing the effects of the degree of urbanisation, forest size, forest management (time since last thinning), disturbance (indicated by path density), canopy closure, litter moisture content, soil organic nitrogen content and species richness of ground vegetation on the microbial activity (log-transformed) at the three sampling dates (early spring, late spring, autumn – after 2, 4, 8 months of incubation, respectively).

	Early spring			Late spring			Autumn		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Degree of urbanisation	2,20	0.69	0.51	2,18	1.63	0.22	2,13	3.09	0.080
Forest size	2,20	1.43	0.26	2,18	7.89	**0.004**	2,13	1.14	0.35
Time since last thinning	–	–	–	2,18	4.17	**0.033**	2.13	6.52	**0.011**
Path density	–	–	–	–	–	–	1,13	13.97	**0.003**
Canopy closure	–	–	–	–	–	–	–	–	–
Moisture content of litter [a]	1,49	22.08	< **0.001**	1,46	252.92	< **0.001**	1.44	21.04	< **0.001**
Soil organic nitrogen content	–	–	–	–	–	–	–	–	–
Species richness of ground vegetation [a]	–	–	–	1,46	5.03	**0.030**	–	–	–
Degree of urbanisation*forest size	–	–	–	–	–	–	4.13	3.45	**0.039**

Significant *P* values (< 0.05) are in bold.

– Factor was excluded from the model by step-wise reduction

[a] sqrt-transformed.

native species by human activity (McKinney, 2002; Kühn et al., 2004; Kowarik, 2011). In our study, however, plant species richness of ground vegetation decreased with increasing degree of urbanisation. This could be explained by the very low number of non-native species (6 of 88 species; 6.8%) found in the forest sites examined, which might not compensate the general loss of species caused by urban development.

In contrast to our expectations, plant species richness of ground vegetation was not influenced by the size of forests. This finding was even more surprising, because many small forest sites were planted in the last 130 years and thus are relatively young. However, most of them were within close proximity to larger forests (15–1300 m; mean: 414 m), which might have served as source for propagules colonising small forest patches in their surroundings. Another possible explanation is that the establishment of open-land species originating from the surrounding matrix contributes to the comparatively high number of species in small forests. In our study, however, the number of open-land species was similar among the three forest size classes (Table S2). Our findings indicate that small forests still harbour a vegetation community typical for this region – even in densely settled areas. The lack of response of plant species richness to forest size may also correspond to a "small fragment" effect (MacArthur and Wilson, 1967). This theory states that below a certain forest size, species richness depends on environmental characteristics such as landscape structure, disturbance and human impact rather than area per se (Triantis et al., 2006).

4.2. Decomposition rate

Decomposition rates of leaf litter are influenced by several factors including site environment, decomposer organisms and the quality of leaf litter (Swift et al., 1979). By using reference litter, we were able to keep litter quality constant (Pouyat et al., 1997). Therefore, variations in decomposition recorded in our study can either be attributed to forest or to plot characteristics.

The percentage of mass loss in *F. sylvatica* leaves recorded in our study after 8 months (Table S5 and S6) was similar to those reported by Anderson (1973) and Jacob et al. (2010) in rural landscapes. However, any comparison of loss of litter mass in *F. sylvatica* across studies should be done with caution because of differences in preparation, mesh size of bags, incubation time and tree species composition at the decomposition site (e.g. Anderson, 1973; Jacob et al., 2010; Berger and Berger, 2014).

In our study, the decomposition rate of litter (k_{litter}) of *F. sylvatica* leaves was not influenced by the degree of urbanisation, contradicting the expectation. Studies conducted along urban–rural gradients showed either an increased (Pouyat et al., 1997; Pouyat and Carreiro, 2003; Nikula et al., 2010) or a decreased (Pavao-Zuckerman and Coleman, 2005) rate of litter mass loss in urban forests compared with rural forests. The duration of incubation in these studies ranged from 6 months (Pouyat et al., 1997) up to 36 months (Pavao-Zuckerman and Coleman, 2005). The studies of Nikula et al. (2010) and Pavao-Zuckerman and Coleman (2005) also differed in climatic conditions from our study site, being conducted in boreal, respectively, subtropical forests. Beside differences in the study design and the spatial dimension of the study area, these contrasting findings can be explained by the lower palatability of decaying leaves of *F. sylvatica* compared to the leaves of species considered in other studies (McClaugherty et al., 1985; Cortez, 1998). It is possible that an incubation time of 8 months was too short to detect differences in k_{litter} of *F. sylvatica* between forests located in densely and sparsely settled areas. Furthermore, individual environmental factors in densely settled areas may have different impacts on k_{litter} depending on the size of the forest.

In line with our expectations, k_{litter} was higher in large forests than in the small and medium-sized forest sites examined during the early stage of decomposition. To our knowledge, previous studies did not consider area-related effects on k_{litter}. Our finding may be caused by the observed difference in soil moisture content between large and small forest sites (see above), which has been shown to influence decomposition processes (Pavao-Zuckerman and Coleman, 2005; Riutta et al., 2012).

When the combined effects of forest size and the percentage cover of sealed areas in their surroundings are considered, then we found lower k_{litter} values in large forests than in small and medium-sized forests located in areas with high degree of urbanisation. This indicates that abiotic and biotic site characteristics of forests of similar size differently influenced k_{litter} depending on the degree of urbanisation in their surroundings. In this way, decay-promoting factors such as the increased soil pH found in the small and medium-sized forest sites examined may have counteracted the negative effects of urbanisation, which may have caused the lower k_{litter} values in large forest sites. Surprisingly, soil temperature did not differ among the three classes of degree of urbanisation and forest size, as higher temperatures have been reported to stimulate decomposer activity in other studies (Pouyat et al., 1997; Pouyat and Carreiro, 2003).

The initial concentrations of the assessed chemical litter characteristics of *F. sylvatica* leaves were in the range of measurements reported (e.g. Anderson, 1973; Jacob et al., 2010). In contrast to k_{litter}, the decomposition rates of lignin (k_{lignin}) was neither influenced by degree of urbanisation nor by forest size in contrast to our expectations. Since invertebrates do not have the enzymatic ability to digest lignin, differences in microbial activity among forests may have caused this discrepancy (Berg and McClaugherty, 2014). Indeed, k_{lignin} increased with soil moisture content, similar to microbial activity, which was positively affected by litter moisture content (see below).

4.3. Microbial activity

The enzymatic breakdown of leaf litter mediated by bacteria and fungi plays an important role in the early stage of decomposition (McClaugherty and Berg, 2011). In our study, moisture content of litter was the best predictor of microbial activity, followed by forest characteristics including size. Beside soil moisture, plant species richness influenced microbial activity. However, this was only the case in late spring. This result could be due to the seasonal variation in plant species richness in the forests being highest in late spring. Furthermore, this result is in line with the findings of several studies showing that microbial community biomass, respiration and catabolic activity was positively related to plant species richness (Zak et al., 2003; Liu et al., 2008; Lange et al., 2014). Given that microbial biomass varies greatly both spatially and temporarily at a small scale (McClaugherty and Berg, 2011), mechanisms associated with degree of urbanisation may be too coarse to detect differences in microbial activity.

Variations in microclimatic conditions may also be the underlying cause of the combined effects of degree of urbanisation and forest size on microbial activity detected in early autumn. During our study, the summer months were relatively warm and abnormally dry. As a consequence, the moisture content of leaf litter was low causing a decline in microbial activity (Table S5 and S6). This effect was most pronounced in small and medium-sized forests in densely settled areas, as litter moisture content decreased with increasing degree of urbanisation. In large forest sites, however, microbial activity showed little change, probably due to the slightly lower soil temperature and higher soil moisture content recorded in these sites.

5. Conclusions

Our study revealed combined effects of the degree of urbanisation and forest size on the decomposition rate of *F. sylvatica* in the early stage of decomposition. This finding highlights that even small urban forests can contribute to local plant diversity and important ecosystem functions including the decomposition of leaf litter. We, therefore, recommend that urban planners also consider small forests in their concepts of green area management. Our results also showed that moisture contents of soil and litter were important determinants in the decomposition processes of leaf litter. Therefore, locally adapted management strategies to protect the leaf litter layer from various types of disturbances (recreational use, thinning) and to reduce depth-of-edge influence can promote biological activity in soil. As primary products in temperate forests enter food webs mainly as dead organic matter (Swift et al., 1979; Cebrian and Lartigue, 2004), maintaining the diversity and feeding activity of decomposers may also be beneficial for species at higher trophic levels.

Acknowledgement

We thank A. Baur, B. Braschler and two anonymous reviewers for comments on the manuscript and R. Schneider, H. Tan, D. Binggeli, F. Toscan and K. Reinacher for helping to analyse the litter and soil characteristics. Financial support was received from the Stadtgärtnerei Basel.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ufug.2017.10.009.

References

Allen, S.E., 1989. Chemical Analysis of Ecological Material, 2nd ed. Blackwell Scientific, Oxford.

Anderson, J.M., 1973. The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. Oecologia 12, 275–288. http://dx.doi.org/10.1007/BF00347567.

Berg, B., McClaugherty, C., 2014. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration, 2nd ed. Springer, Heidelberg. http://dx.doi.org/10.1007/978-3-642-38821-7.

Berger, T.W., Berger, P., 2014. Does mixing of beech (*Fagus sylvatica*) and spruce (*Picea abies*) litter hasten decomposition? Plant Soil 377, 217–234. http://dx.doi.org/10.1007/s11104-013-2001-9.

Blair, J.M., 1988. Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. Soil Biol. Biochem. 20, 693–701. http://dx.doi.org/10.1016/0038-0717(88)90154-X.

Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech a review. Forestry 80, 413–429. http://dx.doi.org/10.1093/forestry/cpm028.

Bolund, P., Hunhammer, S., 1999. Ecosystem services in urban areas. Ecol. Econ. 29, 293–301. http://dx.doi.org/10.1016/S0921-8009(99)00013-0.

Braun-Blanquet, J., 1964. Pflanzensoziologie: Grundzüge der Vegetationskunde. Springer, New York. http://dx.doi.org/10.1007/978-3-7091-8110-2.

Bremner, J.M., 1965. Total nitrogen. In: Black, C.A. (Ed.), Methods of Soil Analysis. Part 2. American Society of Agronomy, Madison, pp. 1149–1178. http://dx.doi.org/10.2134/agronmonogr9.2.c32.

Burnand, J., Hasspacher, B., 1999. Waldstandorte beider Basel. Quellen und Forschungen zur Geschichte und Landeskunde des Kantons Basel-Landschaft, Band 72. Liestal, Verlag des Kantons Basel-Landschaft.

Cebrian, J., Lartigue, J., 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol. Monogr. 7, 237–259. http://dx.doi.org/10.1890/03-4019.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. Science 277, 500–504. http://dx.doi.org/10.1126/science.277.5325.500.

Cortez, J., 1998. Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. Soil Biol. Biochem. 30, 783–793. http://dx.doi.org/10.1016/S0038-0717(97)00163-6.

Cotrufo, M.F., DeSanto, A.V., Alfani, A., Bartoli, G., DeCristofaro, A., 1995. Effects of urban heavy metal pollution on organic matter decomposition in *Quercus ilex* L. woods. Environ. Pollut. 89, 81–87. http://dx.doi.org/10.1016/0269-7491(94)00041-B.

Crawley, M.J., 2007. The R Book. Wiley, Chichester, England. http://dx.doi.org/10.1002/9780470515075.

Dick, R.P., Breakwell, D.P., Turco, R.F., 1996. Soil enzyme activities and biodiversity measurements as integrative microbiological indicators. In: Doran, J.W., Jones, A.J. (Eds.), Methods of Assessing Soil Quality. SSSA Special Publication 49. Soil Science Society of America, Madison, USA, pp. 247–271. http://dx.doi.org/10.2136/sssaspecpub49.c15.

Dwyer, J.F., McPherson, E.G., Schroeder, H.W., Rowntree, R., 1992. Assessing the benefits and costs of the urban forest. J. Arboric. 18, 227–234.

Enloe, H.A., Lockaby, B.G., Zipperer, W.C., Somers, G.L., 2015. Urbanization effects on leaf litter decomposition, foliar nutrient dynamics and aboveground net primary productivity in the subtropics. Urban Ecosyst. 18, 1285–1303. http://dx.doi.org/10.1007/s11252-015-0444-x.

Gehlhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecol. 147, 21–35. http://dx.doi.org/10.1023/A:1009846507652.

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. http://dx.doi.org/10.1126/science.1150195.

Hamberg, L., Lehvävirta, S., Kotze, D.J., 2009. Forest edge structure as a shaping factor of understorey vegetation in urban forests in Finland. For. Ecol. Manage. 257, 712–722. http://dx.doi.org/10.1016/j.foreco.2008.10.003.

Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302–1305. http://dx.doi.org/10.1890/0012-9615(1998)068[0121:EOPCAD]2.0.CO;2.

Jacob, M., Viedenz, K., Polle, A., Thomas, F.M., 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). Oecologia 164, 1083–1094. http://dx.doi.org/10.1007/s00442-010-1699-9.

Kühn, I., Brandl, R., Klotz, S., 2004. The flora of German cities is naturally species rich. Evol. Ecol. Res. 6, 749–764.

Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. Environ. Pollut. 159, 1974–1983. http://dx.doi.org/10.1016/j.envpol.2011.02.022.

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2014. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707. http://dx.doi.org/10.1038/ncomms7707. (8pp).

Liu, Z., Liu, G., Fu, B., Zheng, X., 2008. Relationship between plant species diversity and soil microbial functional diversity along a longitudinal gradient in temperate grasslands of Hulunbeir, Inner Mongolia, China. Ecol. Res. 23, 511–518. http://dx.doi.org/10.1007/s11284-007-0405-9.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Monographs in Population Biology. Princeton University Press, Princeton, NJ.

Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biol. Conserv. 66, 185–194 https://doi.org/10.1016/0006-3207(93)90004-K.

McClaugherty, C.A., Berg, B., 2011. Soils and decomposition. eLS, 2011, John Wiley & Sons, Ltd. http://dx.doi.org/10.1002/9780470015902.a0003187.pub2.

McClaugherty, C.A., Pastor, J., Aber, J.D., Melillo, J.M., 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66, 266–275. http://dx.doi.org/10.2307/1941327.

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 Ecol. 23, 1143–1155. http://dx.doi.org/10.1007/s10980-008-9253-4.

McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M., Medley, K., 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosyst. 1, 21–36. http://dx.doi.org/10.1023/A:1014359024275.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. Bioscience 52, 883–890. http://dx.doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2.

Melliger, R.L., Rusterholz, H.-P., Baur, B., 2017. Habitat- and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape. Urban Ecosyst. 20, 1095–1107. http://dx.doi.org/10.1007/s11252-017-0662-5.

MeteoSwiss, 2015. Climate Normals Basel/Binningen, Reference Period 1981–2010. Federal office of meteorology and climatology MeteoSwiss(http://www.meteoswiss.admin.ch. Accessed 26 May 2016).

Moreira-Vilar, F.C., Siqueira-Soares, R.D., Finger-Teixeira, A., de Oliveira, D.M., Ferro, A.P., da Rocha, G.J., Ferrarese, M.D.L., dos Santos, W.D., Ferrarese-Filho, O., 2014. The acetyl bromide method is faster, simpler and presents best recovery of lignin in different herbaceous tissues than klason and thioglycolic acid methods. PLoS One 9, 1–7. http://dx.doi.org/10.1371/journal.pone.0110000.

Niemelä, J., 1999. Ecology and urban planning. Biodivers. Conserv. 8, 119–131. http://dx.doi.org/10.1023/A:1008817325994.

Nikula, S., Vapaavouri, E., Manninen, S., 2010. Urbanization-related changes in European aspen (*Populus tremula* L.): leaf traits and litter decomposition. Environ. Pollut. 158, 2132–2142. http://dx.doi.org/10.1016/j.envpol.2010.02.025.

Pavao-Zuckerman, M.A., Coleman, D.C., 2005. Decomposition of chestnut oak (*Quercus prinus*) leaves and nitrogen mineralization in an urban environment. Biol. Fertil. Soils 41, 343–349. http://dx.doi.org/10.1007/s00374-005-0841-z.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E., Kaushal, S.S., Marshall, V., McGrath, B.P., Nilon, C.H., Pouyat, R.V., Szlavecz, K., Troy, A., Warren, P., 2011. Urban ecological systems: scientific foundations and a decade of progress. J. Environ. Manage. 92, 331–362. http://dx.doi.org/10.1016/j.jenvman.2010.08.022.

Pouyat, R.V., Carreiro, M.M., 2003. Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban–rural land-use gradient. Oecologia 135, 288–298. http://dx.doi.org/10.1007/s00442-003-1190-y.

Pouyat, R.V., McDonnell, M.J., Pickett, S.T.A., 1997. Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. Urban Ecosyst. 1, 117–131. http://dx.doi.org/10.1023/A:1018567326093.

R Development Core Team, 2013. R: a Language and Environment for Statistical Computing, Version 3.0.2. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Riutta, T., Slade, E.M., Bebber, D.P., Taylor, M.E., Malhi, Y., Riordan, P., Macdonald, D.W., Morecroft, M.D., 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biol.

Biochem. 49, 124–131. http://dx.doi.org/10.1016/j.soilbio.2012.02.028.

Schnürer, J., Rosswall, T., 1982. Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. Appl. Environ. Microbiol. 43, 1256–1261.

Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.A., Soltanpour, P.N., Tabatabai, M.A., Jhonston, C.T., Sumner, M.E., 1996. Methods of Soil Analysis, Part 3, Chemical Methods, 3rd ed. ASA, Madison. http://dx.doi.org/10.2136/sssabookser5.3.c32.

Statistisches Amt Kanton Basel-Stadt, 2015. Tabellen: Bevölkerung; Bodennutzung; Pendler. (http://www.statistik.bs.ch/zahlen/tabellen.html. Accessed 26 May 2016).

Sukopp, H., 1998. Urban ecology: scientific and practical aspects. In: Breuste, J., Feldmann, H., Uhlmann, O. (Eds.), Urban Ecology. Springer Verlag, Berlin, pp. 3–16. http://dx.doi.org/10.1007/978-3-642-88583-9.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley, CA.

Triantis, K.A., Vardinoyannis, K., Tsolaki, E.P., Botsaris, I., Lika, K., Mylonas, M., 2006. Re-approaching the small island effect. J. Biogeogr. 33, 914–923. http://dx.doi.org/10.1111/j.1365-2699.2006.01464.x.

Vallet, J., Beaujouan, V., Pithon, J., Rozé, F., Daniel, H., 2010. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. Biodivers. Conserv. 19, 3375–3392. http://dx.doi.org/10.1007/s10531-010-9901-2.

Wieder, R.K., Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63, 1636–1642. http://dx.doi.org/10.2307/1940104.

Xuluc-Tolosa, F.J., Vester, H.F.M., Ramírez-Marcial, N., Castellanos-Albores, J., Lawrence, D., 2003. Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. For. Ecol. Manage. 174, 401–412. http://dx.doi.org/10.1016/S0378-1127(02)00059-2.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84, 2042–2050. http://dx.doi.org/10.1890/02-0433.

Supplementary material Chapter III

Table S1	Characteristics of the 25 forests examined
Table S2	Species list of vascular plants
Table S3	Ground vegetation and soil characteristics of forests, which differed in the degree of urbanisation and size
Table S4	Mean soil surface temperature of forests, which differed in the degree of urbanisation and size
Table S5	Litter characteristics and microbial activity in forests located in areas with different degrees of urbanisation
Table S6	Litter characteristics and microbial activity in forests located in areas of different size

Figure S1	Mean soil surface temperature in forests
Figure S2	Scatter plots of significant effects in k_{litter} and k_{lignin}
Figure S3	Bar plots and scatter plots of the significant differences in microbial activity

Table S1

Characteristics of the 25 forests examined in Basel (Switzerland) and its surrounding.

Forest	Coordinates	Forest history[1]	Forest vegetation[2]	Elevation (m a.s.l.)	Exposure[3]	Area (m^2)	Area (in classes)	% sealed area (r = 500 m)	Sealed (in classes)	Time since last thinning (in y)	Density of paths (m/ha)
BS1	47° 34' 34.58" N 7° 36' 19.23" E	Forest	Galio-Carpinetum Corydalidetosum Solidae	269	–	21000	Large	20	Medium	2	360.6
BS2	47° 34' 20.76" N 7° 36' 52.84" E	Planted	Galio-Carpinetum Corydalidetosum Solidae	263	–	620	Small	22	Medium	20	580.6
BS3	47° 34' 20.65" N 7° 37' 11.82" E	Planted	Galio-Carpinetum Corydalidetosum Solidae	265	–	4576	Medium-sized	12	Low	9	243.2
BS4	47° 33' 45.65" N 7° 37' 44.02" E	Planted	Ulmo-Fraxinetum Listeretosum	262	S	7458	Medium-sized	19	Medium	>20	311.6
BS5	47° 33' 12.30" N 7° 36' 51.09" E	Planted	Galio Odorati-Fagetum Cornetosum	262	NE	7049	Medium-sized	39	High	3	283.7
BS6	47° 32' 43.72" N 7° 36' 26.85" E	Planted	Aro-Fagetum	276	–	1084	Small	70	High	14	48.0
BS7	47° 32' 30.99" N 7° 35' 2.33" E	Fragment	–	299	NNE	19000	Large	37	High	1	466.2
BS8	47° 32' 8.70" N 7° 35' 23.09" E	Fragment	Galio Odorati-Fagetum Cornetosum	326	E	3009	Small	31	High	1	254.6
BS9	47° 32' 17.69" N 7° 35' 38.71" E	Planted	Aro-Fagetum	303	NNE	2285	Small	43	High	3	337.0
BS10	47° 31' 57.55" N 7° 36' 11.58" E	Fragment	Galio Odorati-Fagetum Typicum	338	NW	14000	Large	44	High	6	445.9
BS11	47° 31' 47.76" N 7° 35' 49.19" E	Fragment	Galio Odorati-Fagetum Typicum	370	E	21000	Large	23	Medium	9	410.3
BS12	47° 31' 26.26" N 7° 35' 33.76" E	Fragment	Galio Odorati-Fagetum Typicum	314	–	19400	Large	14	Low	4	319.1
BS13	47° 31' 46.44" N 7° 36' 12.24" E	Planted	–	376	NW	3633	Small	46	High	16	715.7

Forest	Coordinates	Forest history[1]	Forest vegetation[2]	Elevation (m a.s.l.)	Exposure[3]	Area (m^2)	Area (in classes)	% sealed area (r = 500 m)	Sealed (in classes)	Time since last thinning (in y)	Density of paths (m/ha)
BS14	47° 35' 33.14” N 7° 40' 41.10” E	Forest	Galio Odorati-Fagetum Cornetosum	473	SW	34000	Large	3	Low	>20	23.0
BS15	47° 35' 15.09” N 7° 40' 2.90” E	Planted	Galio Odorati-Fagetum Typicum	346	S	2800	Small	10	Low	7	114.3
BS16	47° 35' 5.71” N 7° 40' 9.23” E	Planted	Galio Odorati-Fagetum Pulmonarietosum	330	SSE	4061	Medium-sized	8	Low	3	448.2
BS17	47° 35' 18.09” N 7° 38' 52.08” E	Planted	–	273	–	258	Small	17	Medium	>20	658.9
BS18	47° 34' 30.78” N 7° 40' 35.28” E	Forest	Galio Odorati-Fagetum Cornetosum	487	–	14000	Large	4	Low	1	80.0
BS19	47° 34' 25.90" N 7° 39' 53.22" E	Forest	Galio Odorati-Fagetum Cornetosum	450	NW	50000	Large	10	Low	>20	151.4
BS20	47° 34' 29.73" N 7° 39' 29.56" E	Fragment	Galio Odorati-Fagetum Cornetosum	384	NW	36000	Large	12	Low	11	557.6
BS21	47° 34' 51.72" N 7° 39' 37.41" E	Fragment	Carici Remotae-Fraxinetum Typicum	302	–	4686	Medium-sized	16	Medium	15	200.6
BS22	47° 34' 0.42" N 7° 38' 22.88" E	Planted	–	277	–	4234	Medium-sized	24	Medium	1	571.6
BS23	47° 33' 58.73" N 7° 38' 46.35" E	Planted	–	309	S	1500	Small	14	Low	1	0.0
BS24	47° 33' 50.63" N 7° 38' 42.82" E	Forest	Galio Odorati-Fagetum Pulmonarietosum	319	NNW	4034	Medium-sized	12	Low	1	210.7
BS25	47° 34' 7.38" N 7° 39' 4.87" E	Forest	Galio-Fagetum Pulmonarietosum, Stachys Ausbildung	363	WNW	8908	Medium-sized	12	Low	2	264.6

---

[1] Forest = Part of a large continuous forest; Fragment = remnant of a former large continuous forest; Planted = forest site was planted after 1884 or was a result of abandonment

[2] Burnand, J., Hasspacher, B., 1999. Waldstandorte beider Basel. Quellen und Forschungen zur Geschichte und Landeskunde des Kanton Basel-Landschaft, Band 72. Verlag des Kantons Basel-Landschaft, Liestal.

[3] Exposure was determined for forest sites situated on a slope.

Table S2

Species list of vascular plants. The occurrence in the forests examined and the plant functional groups are given.

Species	Functional group	BS1	BS2	BS3	BS4	BS5	BS6	BS7	BS8	BS9	BS10	BS11	BS12	BS13
Acer campestre	Woody	0	0	0	0	1	0	0	1	1	0	0	1	1
Acer platanoides	Woody	1	1	1	1	1	1	1	1	1	1	1	1	1
Acer pseudoplatanus	Woody	1	1	1	1	1	1	1	1	1	1	1	1	1
Aegopodium podagraria	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Aesculus hippocastanum	Woody	0	0	0	1	0	0	0	0	0	0	0	0	0
Agrostis capillaris	Grass	0	0	0	1	0	0	0	0	0	0	0	0	0
Agrostis gigantea	Grass	0	0	0	0	0	0	0	0	0	0	0	1	0
Alliaria petiolata	Forb	1	0	1	1	0	0	0	0	0	0	0	0	0
Allium sp.	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Allium ursinum	Forb	1	0	0	0	0	0	1	1	1	0	0	0	0
Anemone nemorosa	Forb	0	0	0	0	0	0	0	0	0	1	0	0	0
Arum maculatum	Forb	1	1	1	0	0	0	1	0	0	0	0	0	0
Berberis vulgaris	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachypodium pinnatum	Grass	0	0	0	1	0	0	0	0	0	0	0	0	0
Brachypodium sylvaticum	Grass	0	1	0	0	0	0	0	0	0	0	0	1	0
Buxus sempervirens	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pendula	Grass	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex remota	Grass	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex sylvatica	Grass	0	1	0	0	0	0	0	0	0	1	1	1	0
Carpinus betulus	Woody	1	1	1	0	1	1	1	1	0	1	1	1	0
Castanea sativa	Woody	0	1	0	0	0	0	0	0	0	0	0	0	0
Circaea lutetiana	Forb	1	1	0	0	0	0	1	1	1	0	0	1	0
Clematis vitalba	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus sanguinea	Woody	0	0	0	1	0	1	1	1	0	0	0	1	1
Corylus avellana	Woody	0	1	0	1	1	0	0	0	0	1	0	1	1
Cotoneaster tomentosus	Woody	0	0	0	0	0	0	0	0	0	0	0	0	1
Crataegus laevigata	Woody	0	1	0	0	0	0	0	0	0	0	0	0	0
Crataegus monogyna	Woody	0	1	0	1	0	0	0	0	0	0	0	0	0
Dactylis glomerata	Grass	0	0	0	0	1	0	0	0	0	0	0	1	0
Dactylis polygama	Grass	0	1	0	0	0	0	1	0	0	0	0	0	0

Species	Functional group	BS1	BS2	BS3	BS4	BS5	BS6	BS7	BS8	BS9	BS10	BS11	BS12	BS13
Daphne laureola	Woody	0	0	0	0	0	0	0	0	0	0	0	0	1
Dryopteris filix-mas	Forb	0	0	0	0	0	0	0	0	0	1	0	0	0
Duchesnea indica	Forb	0	0	0	0	0	0	0	0	1	0	1	1	0
Epilobium parviflorum	Forb	0	0	0	0	0	0	0	1	0	0	0	0	0
Euonymus europaeus	Woody	1	0	1	0	0	0	1	0	0	1	0	0	0
Euphorbia amygdaloides	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Fagus sylvatica	Woody	1	0	1	0	0	0	1	0	1	1	1	1	0
Fragaria vesca	Forb	0	1	0	0	0	0	0	0	0	0	0	0	0
Fraxinus excelsior	Woody	1	1	1	1	1	0	1	1	1	1	1	1	1
Galeopsis tetrahit	Forb	0	0	1	0	0	0	0	0	0	0	0	0	0
Galium odoratum	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium spurium	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium robertianum	Forb	0	0	1	0	0	0	0	1	0	0	0	0	0
Geum urbanum	Forb	1	1	1	1	1	0	1	1	1	1	1	1	1
Glechoma hederacea	Forb	0	0	1	0	0	0	1	1	0	0	0	0	0
Hedera helix	Forb/Woody	1	1	1	1	1	1	1	1	1	1	1	1	1
Helleborus foetidus	Forb	0	0	0	1	0	0	0	0	0	0	0	0	0
Heracleum sphondylium	Forb	0	0	0	0	1	0	0	1	0	0	0	0	0
Ilex aquifolium	Woody	0	0	0	0	1	0	1	0	1	0	0	0	0
Impatiens parviflora	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Juglans regia	Woody	0	0	1	0	0	0	0	0	0	0	0	1	1
Lamium argentatum	Forb	0	0	0	0	1	0	0	0	0	0	0	1	0
Lamium galeobdodon	Forb	1	0	0	1	1	0	0	1	0	0	0	0	0
Lathyrus vernus	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Ligustrum vulgare	Woody	0	0	1	0	1	1	0	0	0	0	0	1	1
Lonicera xylosteum	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Luzula sylvatica	Grass	0	0	0	0	0	0	0	0	0	0	0	1	0
Mahonia aquifolium	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Maianthemum bifolium	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Paris quadrifolia	Forb	0	0	0	0	0	0	0	0	0	1	0	0	0
Phyteuma spicatum	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonatum multiflorum	Forb	1	0	0	0	0	0	1	0	0	0	0	1	0

Species	**Functional group**	**BS1**	**BS2**	**BS3**	**BS4**	**BS5**	**BS6**	**BS7**	**BS8**	**BS9**	**BS10**	**BS11**	**BS12**	**BS13**
Prunus avium	Woody	0	1	0	1	0	0	0	0	0	0	0	1	0
Prunus laurocerasus	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus padus	Woody	0	1	0	1	0	0	0	0	1	0	0	1	0
Prunus serotina	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus petraea	Woody	0	0	0	0	0	0	0	0	0	0	1	1	0
Quercus robur	Woody	1	1	1	0	0	0	1	1	1	1	1	0	1
Quercus rubra	Woody	0	0	0	0	0	0	1	0	0	0	0	0	0
Ranunculus auricomus	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus ficaria	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes rubrum	Woody	0	0	0	0	0	1	0	1	0	1	0	0	0
Ribes uva-crispa	Woody	0	0	0	0	1	0	0	0	0	1	1	1	1
Rosa sp.	Forb/Woody	0	0	0	0	0	0	0	0	1	0	0	0	0
Rubus sp.	Forb	1	0	1	1	1	0	1	1	1	1	1	1	1
Rumex sp.	Forb	1	0	0	0	0	0	0	0	0	0	0	0	0
Sambucus nigra	Woody	1	0	0	0	0	0	1	0	0	0	0	0	0
Stachys sylvatica	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Taxus baccata	Woody	0	0	0	0	0	1	0	0	0	0	0	0	0
Tilia platyphyllos	Woody	1	1	0	0	1	0	1	0	1	1	0	0	1
Ulmus glabra	Woody	0	0	0	1	1	1	1	0	1	0	0	0	0
Urtica dioica	Forb	1	0	0	0	0	0	0	0	1	0	0	0	0
Veronica montana	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum lantana	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	Woody	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicia sepium	Forb	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola reichenbachiana	Forb	0	0	0	0	0	0	0	0	0	0	0	1	0
Total number of species per forest		**20**	**20**	**17**	**18**	**18**	**9**	**22**	**18**	**18**	**18**	**13**	**27**	**16**

Table S2 *continued*

Species	**Functional group**	**BS14**	**BS15**	**BS16**	**BS17**	**BS18**	**BS19**	**BS20**	**BS21**	**BS22**	**BS23**	**BS24**	**BS25**	**Frequency of occurrence**
Acer campestre	Woody	1	1	1	1	1	0	0	1	0	1	1	1	**14**
Acer platanoides	Woody	1	1	0	1	0	1	1	0	1	1	1	1	**22**
Acer pseudoplatanus	Woody	1	1	0	0	0	0	1	1	1	1	1	1	**21**
Aegopodium podagraria	Forb	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Aesculus hippocastanum	Woody	0	0	1	0	0	0	0	0	0	0	0	0	**2**
Agrostis capillaris	Grass	0	0	0	1	0	0	0	0	0	0	0	0	**2**
Agrostis gigantea	Grass	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Alliaria petiolata	Forb	1	0	0	1	0	0	0	0	0	1	0	0	**6**
Allium sp.	Forb	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Allium ursinum	Forb	0	0	0	0	0	0	0	1	0	0	1	0	**6**
Anemone nemorosa	Forb	1	0	0	0	1	1	1	1	0	0	1	1	**8**
Arum maculatum	Forb	0	0	1	0	0	0	1	1	0	0	1	1	**9**
Berberis vulgaris	Woody	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Brachypodium pinnatum	Grass	0	0	0	0	0	0	0	0	0	1	0	0	**2**
Brachypodium sylvaticum	Grass	1	1	0	1	1	0	0	0	1	1	1	0	**9**
Buxus sempervirens	Woody	0	0	0	0	0	0	0	0	1	1	0	0	**2**
Carex pendula	Grass	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Carex remota	Grass	0	0	0	0	0	0	0	0	1	0	0	0	**1**
Carex sylvatica	Grass	1	0	0	0	1	0	1	0	0	0	0	0	**7**
Carpinus betulus	Woody	1	0	1	0	1	1	1	0	1	1	0	1	**18**
Castanea sativa	Woody	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Circaea lutetiana	Forb	1	1	1	0	0	0	0	1	0	1	1	1	**13**
Clematis vitalba	Woody	0	1	0	1	0	0	0	0	0	0	0	0	**2**
Cornus sanguinea	Woody	1	0	1	0	1	0	0	0	0	1	0	0	**10**
Corylus avellana	Woody	0	1	1	0	1	1	1	1	1	1	0	1	**15**
Cotoneaster tomentosus	Woody	0	0	0	1	0	0	0	0	0	0	0	0	**2**
Crataegus laevigata	Woody	1	0	0	1	0	1	0	0	0	0	0	0	**4**
Crataegus monogyna	Woody	0	0	1	1	0	1	0	0	0	0	0	0	**5**
Dactylis glomerata	Grass	0	0	0	0	0	0	0	0	0	1	0	0	**3**
Dactylis polygama	Grass	0	0	0	1	0	0	0	0	0	0	0	0	**3**

Species	**Functional group**	**BS14**	**BS15**	**BS16**	**BS17**	**BS18**	**BS19**	**BS20**	**BS21**	**BS22**	**BS23**	**BS24**	**BS25**	**Frequency of occurrence**
Daphne laureola	Woody	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Dryopteris filix-mas	Forb	0	0	0	0	0	0	0	1	0	0	0	1	**3**
Duchesnea indica	Forb	0	0	0	0	0	0	0	0	0	1	1	1	**6**
Epilobium parviflorum	Forb	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Euonymus europaeus	Woody	0	1	1	0	1	0	0	1	1	1	1	1	**12**
Euphorbia amygdaloides	Forb	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Fagus sylvatica	Woody	1	0	0	0	1	1	1	0	0	1	1	1	**14**
Fragaria vesca	Forb	1	0	0	0	0	0	0	0	0	0	0	0	**2**
Fraxinus excelsior	Woody	1	1	1	1	1	1	1	1	1	1	1	1	**24**
Galeopsis tetrahit	Forb	0	0	1	0	0	0	0	0	0	0	0	0	**2**
Galium odoratum	Forb	1	1	0	0	1	1	0	0	0	0	1	0	**5**
Galium spurium	Forb	1	1	0	1	0	0	0	1	0	0	0	0	**4**
Geranium robertianum	Forb	0	0	0	0	0	0	0	0	0	1	0	0	**3**
Geum urbanum	Forb	1	1	1	1	0	0	0	1	1	1	1	1	**21**
Glechoma hederacea	Forb	1	0	0	1	0	0	0	0	1	1	0	0	**7**
Hedera helix	Forb/Woody	1	1	1	1	1	1	1	1	1	1	1	1	**25**
Helleborus foetidus	Forb	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Heracleum sphondylium	Forb	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Ilex aquifolium	Woody	1	0	0	0	1	1	1	0	1	1	1	1	**11**
Impatiens parviflora	Forb	1	1	0	0	0	0	0	0	0	0	0	0	**2**
Juglans regia	Woody	1	0	0	0	0	0	0	0	0	1	0	0	**5**
Lamium argentatum	Forb	0	0	1	0	0	0	0	1	1	0	1	0	**6**
Lamium galeobdodon	Forb	0	1	1	0	0	1	0	1	1	1	1	1	**12**
Lathyrus vernus	Forb	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Ligustrum vulgare	Woody	0	0	1	1	1	1	1	0	1	1	1	1	**14**
Lonicera xylosteum	Woody	0	0	0	0	1	0	0	1	0	0	0	0	**2**
Luzula sylvatica	Grass	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Mahonia aquifolium	Woody	0	1	0	1	0	0	0	0	0	0	0	0	**2**
Maianthemum bifolium	Forb	1	0	0	0	0	0	0	0	0	0	1	0	**2**
Paris quadrifolia	Forb	0	0	0	0	1	0	1	0	0	0	0	1	**4**
Phyteuma spicatum	Forb	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Polygonatum multiflorum	Forb	0	1	0	0	1	0	1	0	0	0	0	1	**7**
Prunus avium	Woody	1	1	0	1	1	0	1	1	0	1	0	0	**10**

Species	**Functional group**	**BS14**	**BS15**	**BS16**	**BS17**	**BS18**	**BS19**	**BS20**	**BS21**	**BS22**	**BS23**	**BS24**	**BS25**	**Frequency of occurrence**
Prunus laurocerasus	Woody	0	0	0	0	0	0	0	0	1	1	0	0	**2**
Prunus padus	Woody	0	0	0	1	0	0	0	1	0	0	0	0	**6**
Prunus serotina	Woody	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Quercus petraea	Woody	1	0	0	0	0	0	0	0	0	0	0	0	**3**
Quercus robur	Woody	0	0	1	1	0	1	1	1	1	1	1	1	**18**
Quercus rubra	Woody	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Ranunculus auricomus	Forb	0	0	0	0	0	1	1	0	0	0	1	0	**3**
Ranunculus ficaria	Forb	0	0	0	0	0	0	1	0	0	1	0	1	**3**
Ribes rubrum	Woody	0	1	0	1	0	0	0	1	0	0	0	0	**6**
Ribes uva-crispa	Woody	0	0	0	0	0	0	0	0	0	0	0	0	**5**
Rosa sp.	Forb/Woody	1	0	0	1	1	1	1	0	0	0	0	0	**6**
Rubus sp.	Forb	1	1	1	1	1	0	0	1	1	1	1	0	**20**
Rumex sp.	Forb	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Sambucus nigra	Woody	1	0	0	0	0	0	0	0	0	0	0	1	**4**
Stachys sylvatica	Forb	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Taraxacum officinale	Forb	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Taxus baccata	Woody	0	0	0	1	0	0	0	0	1	1	0	0	**4**
Tilia platyphyllos	Woody	0	0	0	0	0	1	1	0	0	0	1	1	**11**
Ulmus glabra	Woody	0	0	0	0	0	0	0	0	1	0	0	0	**6**
Urtica dioica	Forb	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Veronica montana	Forb	0	0	1	0	0	0	0	0	0	0	1	0	**2**
Viburnum lantana	Woody	0	0	0	1	1	0	0	0	0	0	1	0	**3**
Viburnum opulus	Woody	0	0	0	0	1	0	1	0	0	0	0	1	**3**
Vicia sepium	Forb	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Viola reichenbachiana	Forb	1	0	0	0	1	0	0	0	0	0	1	1	**5**
Total number of species per forest		**30**	**21**	**21**	**25**	**26**	**17**	**21**	**21**	**21**	**34**	**27**	**26**	

Table S3

Ground vegetation (species richness, vegetation cover) and soil characteristics* (soil moisture content, soil pH) of forests, which differed in the degree of urbanisation and size. Data (mean ± SE) are shown for the three sampling periods separately.

	Degree of urbanisation			Forest size				
	Low (N = 11)	Medium (N = 7)	High (N = 7)	Small (N = 8)	Medium-sized (N = 8)	Large (N = 9)	Degree of urbanisation	Forest size
Species richness of ground vegetation[1]	13.2 ± 0.9^{a}	10.7 ± 0.9^{ab}	9.8 ± 0.9^{b}	11.5 ± 1.4	11.5 ± 0.7	11.7 ± 1.0	**$F_{2,20}$ = 3.76, P = 0.041**	$F_{2,20}$ = 0.29, P = 0.75
Cover of ground vegetation (in %)[1]	51.0 ± 6.5	57.1 ± 8.6	60.5 ± 4.8	64.0 ± 6.3^{a}	65.1 ± 4.6^{a}	39.0 ± 5.3^{b}	$F_{2,20}$ = 0.79, P = 0.47	**$F_{2,20}$ = 6.67, P = 0.006**
Soil moisture content[1]								
After 2 months (early spring)	30.8 ± 1.3^{a}	26.0 ± 1.4^{b}	30.8 ± 0.8$^{a(b)}$	28.5 ± 1.3	27.8 ± 0.6	31.6 ± 1.8	**$F_{2,20}$ = 4.53, P = 0.024**	$F_{2,20}$ = 2.03, P = 0.16
After 4 months (late spring)	29.5 ± 1.5$^{(a)b}$	24.6 ± 1.9^{a}	30.6 ± 1.3^{b}	27.4 ± 1.6^{a}	25.9 ± 1.3$^{a(b)}$	31.6 ± 1.8$^{a(b)}$	**$F_{2,20}$ = 4.20, P = 0.030**	**$F_{2,20}$ = 3.51, P = 0.049**
After 8 months (autumn)	23.9 ± 1.3^{a}	19.6 ± 1.9$^{(b)}$	24.4 ± 1.1^{a}	21.8 ± 1.4	21.0 ± 1.3	25.4 ± 1.6	**$F_{2,20}$ = 3.58, P = 0.047**	$F_{2,20}$ = 2.70, P = 0.092
Soil pH[2]								
After 2 months (early spring)	6.5 ± 0.2	6.3 ± 0.4	6.6 ± 0.3	7.0 ± 0.1^{a}	6.7 ± 0.3$^{a(b)}$	5.9 ± 0.2^{b}	χ^2 = 0.19, df = 2, P = 0.91	**χ^2 = 10.42, df = 2, P = 0.005**
After 4 months (late spring)	6.5 ± 0.2	6.4 ± 0.4	6.6 ± 0.2	7.0 ± 0.1^{a}	6.7 ± 0.3$^{a(b)}$	5.9 ± 0.2^{b}	χ^2 = 0.38, df = 2, P = 0.83	**χ^2 = 8.67, df = 2, P = 0.013**
After 8 months (autumn)	6.5 ± 0.2	6.3 ± 0.4	6.6 ± 0.2	7.0 ± 0.1^{a}	6.7 ± 0.3^{a}	5.8 ± 0.2^{b}	χ^2 = 0.52, df = 2, P = 0.77	**χ^2 = 10.08, df = 2, P = 0.006**

Table S3 *continued*

	Degree of urbanisation			Forest size				
	Low (N = 11)	Medium (N = 7)	High (N = 7)	Small (N = 8)	Medium-sized (N = 8)	Large (N = 9)	Degree of urbanisation	Forest size
Soil organic matter content[1]								
After 2 months (early spring)	17.4 ± 1.5	14.8 ± 1.7	18.7 ± 1.9	18.7 ± 1.3	16.6 ± 2.1	15.9 ± 1.7	$F_{2,20}$ = 1.11, P = 0.35	$F_{2,20}$ = 0.62, P = 0.55
After 4 months (late spring)	17.4 ± 1.5	14.5 ± 1.4	19.3 ± 2.0	18.7 ± 1.4	16.6 ± 2.1	16.2 ± 1.7	$F_{2,20}$ = 1.68, P = 0.21	$F_{2,20}$ = 0.37, P = 0.69
After 8 months (autumn)	17.4 ± 1.5	14.4 ± 1.5	19.3 ± 2.1	18.5 ± 1.4	16.8 ± 2.1	16.1 ± 1.7	$F_{2,20}$ = 1.73, P = 0.20	$F_{2,20}$ = 0.37, P = 0.70
Soil organic nitrogen content[1]								
After 2 months (early spring)	0.35 ± 0.03	0.31 ± 0.04	0.40 ± 0.02	0.38 ± 0.03	0.35 ± 0.03	0.35 ± 0.04	$F_{2,20}$ = 1.69, P = 0.21	$F_{2,20}$ = 0.10, P = 0.91
After 4 months (late spring)	0.36 ± 0.03	0.31 ± 0.04	0.42 ± 0.02	0.38 ± 0.03	0.34 ± 0.03	0.36 ± 0.04	$F_{2,20}$ = 3.21, P = 0.062	$F_{2,20}$ = 0.04, P = 0.96
After 8 months (autumn)	0.36 ± 0.03	0.31 ± 0.04	0.41 ± 0.02	0.38 ± 0.03	0.34 ± 0.03	0.36 ± 0.04	$F_{2,20}$ = 2.77, P = 0.087	$F_{2,20}$ = 0.03, P = 0.97
Soil organic phosphorus content[1, 3]								
After 2 months (early spring)	587.0 ± 27.8^{a}	595.6 ± 58.8^{a}	735.7 ± 52.6^{b}	760.2 ± 43.8^{a}	598.6 ± 39.9^{ab}	545.1 ± 26.0^{b}	**$F_{2,20}$ = 4.66, P = 0.022**	**$F_{2,20}$ = 6.46, P = 0.007**
After 4 months (late spring)	617.3 ± 20.9^{a}	661.7 ± 44.6$^{a(b)}$	752.7 ± 47.9^{b}	772.8 ± 41.0^{a}	658.0 ± 27.5$^{a(b)}$	582.8 ± 15.0^{b}	**$F_{2,20}$ = 6.54, P = 0.007**	**$F_{2,20}$ = 9.28, P = 0.001**
After 8 months (autumn)	640.2 ± 37.2	689.8 ± 39.8	750.2 ± 47.9	776.9 ± 37.5^{a}	713.0 ± 38.8^{a}	578.1 ± 19.5^{b}	$F_{2,20}$ = 3.46, P = 0.051	**$F_{2,20}$ = 9.60, P = 0.001**

* Preliminary analyses revealed inter-correlations among soil characteristics. Therefore, total soil organic matter content, total organic nitrogen and total organic phosphorus content of the soil were excluded from the subsequent analyses

Mean values of three sampling plots from each forest were used in the analyses

Analyses of soil characteristics were performed separately for each sampling date

[1] Two-way ANOVA
[2] Kruskal-Wallis
[3] log-transformed

Significant *P* values (<0.05) are in bold

Different letters next to mean ± SE indicate significant differences among classes. Letters in parentheses indicate tendencies between two classes.

N: number of forests

Table S4

Mean soil surface temperature in forests, which differed in the degree of urbanisation and size, measured over the entire study period (March–October 2015; in °C; mean ± SE) and over the spring, summer and autumn periods separately. Kruskal-Wallis test was used to test differences among degrees of urbanisation and forest size classes.

		Degree of urbanisation				Forest size			
	Number of weeks	Low ($N = 5$)	Medium ($N = 2$)	High ($N = 2$)	*Kruskal-test*	Small ($N = 2$)	Medium-sized ($N = 5$)	Large ($N = 2$)	*Kruskal-test*
Spring–Autumn (20.03–06.10.2015)	29	14.19 ± 0.75	13.70 ± 0.69	14.20 ± 0.74	$\chi^2 = 0.48$, $df = 2$, P = 0.79	14.27 ± 0.76	14.31 ± 0.74	13.33 ± 0.70	$\chi^2 = 1.25$, $df = 2$, P = 0.54
Spring (20.03.–28.05.2015)	10	10.05 ± 0.86	9.92 ± 0.77	9.89 ± 0.77	$\chi^2 = 0.03$, $df = 2$, P = 0.98	9.99 ± 0.85	10.26 ± 0.84	9.30 ± 0.77	$\chi^2 = 1.06$, $df = 2$, P = 0.59
Summer (29.05.–27.08.2015)	13	17.33 ± 0.59	16.65 ± 0.52	17.33 ± 0.57	$\chi^2 = 1.49$, $df = 2$, P = 0.47	17.54 ± 0.54	17.40 ± 0.60	16.26 ± 0.52	$\chi^2 = 3.13$, $df = 2$, P = 0.21
Autumn (28.08.–06.10.2015)	6	14.27 ± 1.00	13.61 ± 1.03	14.60 ± 0.99	$\chi^2 = 1.17$, $df = 2$, P = 0.56	14.31 ± 1.02	14.35 ± 1.03	13.70 ± 0.91	$\chi^2 = 0.71$, $df = 2$, P = 0.70

Weekly mean temperatures based on hourly readings were averaged over spring, summer and autumn and the entire investigation period

N indicates the numbers of forests

Degree of urbanisation (low: <15%; medium: 15–30%; high: >30%)

Forest size (small: <4000 m^2; medium-sized: 4000–10000 m^2; large: >10000 m^2)

Table S5

Litter characteristics (concentration and percentage of initial mass) and microbial activity (hydrolyse activity of FDA) in forests located in areas with different degrees of urbanisation. Data (mean ± SE) are shown for the three sampling periods separately.

	Degree of urbanisation			
	Low (N = 11)	Medium (N = 7)	High (N = 7)	
Early spring (2 months)				
Lignin (%) [1]	19.5 ± 0.6	19.8 ± 0.6	21.5 ± 0.3	$F_{2,22} = 2.73$, $P = 0.087$
C (%) [1]	43.2 ± 0.1	43.2 ± 0.3	43.3 ± 0.3	$F_{2,22} = 0.09$, $P = 0.92$
N (%) [1]	0.97 ± 0.01	0.96 ± 0.02	0.97 ± 0.01	$F_{2,22} = 0.27$, $P = 0.77$
C:N [1]	44.5 ± 0.5	45.1 ± 0.7	44.8 ± 0.5	$F_{2,22} = 0.27$, $P = 0.76$
P (µg g^{-1}) [1]	675.5 ± 17.2	659.4 ± 27.5	606.6 ± 21.7	$F_{2,22} = 2.74$, $P = 0.086$
Fluorescein (µg/g) [*, 1]	68.9 ± 3.9	65.2 ± 3.7	64.4 ± 2.4	$F_{2,22} = 0.45$, $P = 0.64$
Percentage (%) of initial mass of				
litter [1]	96.6 ± 1.0	96.1 ± 1.0	94.5 ± 0.5	$F_{2,22} = 1.29$, $P = 0.30$
lignin [1]	94.2 ± 3.7	96.3 ± 3.6	103.1 ± 1.8	$F_{2,22} = 1.73$, $P = 0.20$
C [1]	93.9 ± 1.1	93.6 ± 1.2	92.3 ± .0.7	$F_{2,22} = 0.61$, $P = 0.55$
N [1]	96.6 ± 0.5	94.8 ± 1.9	93.9 ± 1.5	$F_{2,22} = 1.37$, $P = 0.28$
P [1]	64.9 ± 1.5	64.6 ± 1.8	59.6 ± 2.2	$F_{2,22} = 2.46$, $P = 0.11$
Late spring (4 months)				
Lignin (%) [1]	19.0 ± 0.4	18.1 ± 0.5	18.0 ± 0.5	$F_{2,22} = 1.83$, $P = 0.18$
C (%) [1]	41.2 ± 0.4	41.2 ± 0.8	41.5 ± 0.5	$F_{2,22} = 0.07$, $P = 0.93$
N (%) [2]	1.07 ± 0.01	1.07 ± 0.02	1.10 ± 0.02	$\chi^2 = 1.62$, $df = 2$, $P = 0.44$
C:N [1]	38.8 ± 0.5	38.5 ± 1.0	38.0 ± 0.8	$F_{2,22} = 0.28$, $P = 0.76$
P (µg g^{-1}) [1]	649.4 ± 21.0	646.0 ± 27.5	666.0 ± 18.1	$F_{2,22} = 0.20$, $P = 0.82$
Fluorescein (µg/g) [*, 2]	75.1 ± 6.2	71.3 ± 12.3	74.2 ± 5.9	$\chi^2 = 1.63$, $df = 2$, $P = 0.44$
Percentage (%) of initial mass of				
litter [1]	92.1 ± 0.3	93.3 ± 0.6	92.3 ± 0.9	$F_{2,22} = 1.19$, $P = 0.32$
lignin [1]	87.3 ± 1.6	85.4 ± 2.8	84.4 ± 2.4	$F_{2,22} = 0.50$, $P = 0.61$
C [1]	85.5 ± 1.0	86.7 ± 1.8	86.5 ± 1.3	$F_{2,22} = 0.26$, $P = 0.78$
N [2]	101.1 ± 0.7	102.8 ± 2.0	103.9 ± 2.7	$\chi^2 = 0.21$, $df = 2$, $P = 0.90$
P [1]	59.5 ± 1.7	61.4 ± 2.3	63.9 ± 2.2	$F_{2,22} = 1.21$, $P = 0.32$
Autumn (8 months)				
Lignin (%) [1]	16.2 ± 0.3	16.3 ± 0.9	15.9 ± 0.5	$F_{2,22} = 0.12$, $P = 0.89$
C (%) [1]	39.1 ± 0.6	38.7 ± 1.0	39.4 ± 0.7	$F_{2,22} = 0.19$, $P = 0.83$
N (%) [1]	1.19 ± 0.02	1.21 ± 0.03	1.26 ± 0.03	$F_{2,22} = 2.56$, $P = 0.10$
C:N [1]	32.9 ± 0.7	32.4 ± 1.5	31.4 ± 0.8	$F_{2,22} = 0.59$, $P = 0.57$
P (µg g^{-1}) [2]	827.2 ± 41.5	825.8 ± 80.9	866.0 ± 38.7	$\chi^2 = 1.26$, $df = 2$, $P = 0.53$
Fluorescein (µg/g) [*, 1]	50.0 ± 1.5	48.7 ± 1.3	47.4 ± 1.4	$F_{2,22} = 0.83$, $P = 0.45$
Percentage (%) of initial mass of				
litter [1]	86.1 ± 0.9	86.7 ± 1.1	88.7 ± 1.4	$F_{2,22} = 1.42$, $P = 0.26$
lignin [1]	69.3 ± 1.8	71.4 ± 4.7	71.8 ± 3.1	$F_{2,22} = 0.22$, $P = 0.81$
C [1]	75.7 ± 1.4	75.6 ± 2.2	78.9 ± 2.2	$F_{2,22} = 0.96$, $P = 0.40$
N [2]	105.4 ± 1.4	107.2 ± 2.6	114.9 ± 3.6	$\chi^2 = 3.88$, $df = 2$, $P = 0.14$
P [2]	70.9 ± 3.3	73.2 ± 7.4	79.7 ± 4.2	$\chi^2 = 3.78$, $df = 2$, $P = 0.15$

Degree of urbanisation (low: <15%; medium: 15–30%; high: >30%)

[*] Fluorescein = product of FDA hydrolysis – a surrogate for microbial activity

[1] ANOVA, [2] Kruskal-Wallis test

N: number of forest sites

Table S6

Litter characteristics (concentration and percentage of initial mass) and microbial activity (hydrolyse activity of FDA) in forests of different size. Data (mean ± SE) are shown for the three sampling periods separately.

	Forest size			
	Small (N = 8)	Medium-sized (N = 8)	Large (N = 9)	
Early spring (2 months)				
Lignin (%) [1]	20.5 ± 0.6	19.8 ± 0.7	20.2 ± 0.7	$F_{2,22} = 0.26$, $P = 0.77$
C (%) [1]	43.4 ± 0.3	43.0 ± 0.2	43.3 ± 0.2	$F_{2,22} = 0.56$, $P = 0.58$
N (%) [1]	0.97 ± 0.01^{ab}	0.94 ± 0.01^{a}	0.99 ± 0.01^{b}	**$F_{2,22} = 7.72$, $P = 0.003$**
C:N [1]	44.9 ± 0.5^{ab}	45.8 ± 0.5^{a}	43.7 ± 0.4^{b}	**$F_{2,22} = 5.28$, $P = 0.013$**
P (µg g^{-1}) [1]	640.2 ± 33.3	650.3 ± 15.7	663.2 ± 19.3	$F_{2,22} = 0.24$, $P = 0.79$
Fluorescein (µg/g) [*, 1]	63.9 ± 3.2	64.2 ± 2.4	71.2 ± 4.4	$F_{2,22} = 1.42$, $P = 0.26$
Percentage (%) of initial mass of				
litter [1]	96.0 ± 0.9	96.9 ± 1.2	94.8 ± 0.7	$F_{2,22} = 1.27$, $P = 0.30$
lignin [1]	98.6 ± 3.2	97.0 ± 4.1	96.3 ± 3.8	$F_{2,22} = 0.10$, $P = 0.90$
C [1]	93.8 ± 1.1	94.0 ± 1.3	92.4 ± 0.9	$F_{2,22} = 0.63$, $P = 0.54$
N [1]	95.5 ± 1.8	93.5 ± 0.8	96.8 ± 0.9	$F_{2,22} = 2.01$, $P = 0.16$
P [1]	61.8 ± 2.6	64.5 ± 1.4	63.6 ± 1.7	$F_{2,22} = 0.45$, $P = 0.65$
Late spring (4 months)				
Lignin (%) [1]	18.5 ± 0.6	18.9 ± 0.2	18.1 ± 0.5	$F_{2,22} = 0.85$, $P = 0.44$
C (%) [1]	41.9 ± 0.6	40.6 ± 0.6	41.5 ± 0.4	$F_{2,22} = 1.45$, $P = 0.26$
N (%) [2]	1.07 ± 0.01	1.07 ± 0.01	1.09 ± 0.02	$\chi^2 = 0.92$, $df = 2$, $P = 0.63$
C:N [1]	39.2 ± 0.6	38.2 ± 0.9	38.0 ± 0.6	$F_{2,22} = 0.81$, $P = 0.46$
P (µg g^{-1}) [1]	647.6 ± 20.8	642.4 ± 25.5	667.5 ± 21.0	$F_{2,22} = 0.36$, $P = 0.70$
Fluorescein (µg/g) [*, 2]	67.5 ± 6.3	72.9 ± 11.2	80.2 ± 5.6	$\chi^2 = 3.11$, $df = 2$, $P = 0.21$
Percentage (%) of initial mass of				
litter [1]	92.7 ± 0.6	92.6 ± 0.4	92.1 ± 0.7	$F_{2,22} = 0.34$, $P = 0.71$
lignin [1]	85.9 ± 2.7	88.6 ± 1.3	83.6 ± 2.0	$F_{2,22} = 1.49$, $P = 0.25$
C [1]	87.6 ± 1.4	84.8 ± 1.4	86.0 ± 1.0	$F_{2,22} = 1.20$, $P = 0.32$
N [2]	102.0 ± 1.2	101.3 ± 1.0	103.5 ± 2.3	$\chi^2 = 0.08$, $df = 2$, $P = 0.96$
P [1]	60.5 ± 1.8	60.9 ± 2.1	62.3 ± 2.3	$F_{2,22} = 0.20$, $P = 0.82$
Autumn (8 months)				
Lignin (%) [1]	16.1 ± 0.5^{ab}	15.1 ± 0.3^{a}	17.2 ± 0.6^{b}	**$F_{2,22} = 5.02$, $P = 0.016$**
C (%) [1]	39.9 ± 0.7	37.9 ± 0.9	39.3 ± 0.5	$F_{2,22} = 1.97$, $P = 0.16$
N (%) [1]	1.22 ± 0.02	1.21 ± 0.03	1.21 ± 0.03	$F_{2,22} = 0.08$, $P = 0.92$
C:N [1]	32.8 ± 0.9	31.6 ± 1.2	32.6 ± 0.7	$F_{2,22} = 0.45$, $P = 0.64$
P (µg g^{-1}) [2]	848.1 ± 39.5	895.5 ± 76.3	777.1 ± 29.1	$\chi^2 = 2.79$, $df = 2$, $P = 0.25$
Fluorescein (µg/g) [*, 1]	48.7 ± 1.7	50.1 ± 1.2	48.0 ± 1.5	$F_{2,22} = 0.49$, $P = 0.62$
Percentage (%) of initial mass of				
litter [1]	88.2 ± 1.3	85.6 ± 0.8	87.3 ± 1.2	$F_{2,22} = 1.39$, $P = 0.27$
lignin	71.0 ± 2.7^{ab}	65.0 ± 1.5^{a}	75.3 ± 3.2^{b}	**$F_{2,22} = 3.96$, $P = 0.034$**
C [1]	79.2 ± 2.0	73.1 ± 1.6	77.3 ± 1.4	$F_{2,22} = 3.34$, $P = 0.054$
N [2]	110.9 ± 3.1	106.5 ± 2.5	108.4 ± 2.6	$\chi^2 = 0.97$, $df = 2$, $P = 0.61$
P [2]	75.4 ± 3.8	78.3 ± 6.7	68.9 ± 3.4	$\chi^2 = 2.53$, $df = 2$, $P = 0.28$

Forest size classes (small: <4000 m^2; medium: 4000–10000 m^2; large: >10000 m^2)

[*] Fluorescein = product of FDA hydrolysis – a surrogate for microbial activity

[1] ANOVA, [2] Kruskal-Wallis test

Significant P values (<0.05) are in bold. Different letters next to mean ± SE indicate significant differences among classes.

N: number of forest sites

Fig. S1. Mean soil surface temperature in forests, which differed in the degree of urbanisation and size. Weekly mean temperatures are presented from mid-March to early October 2015.

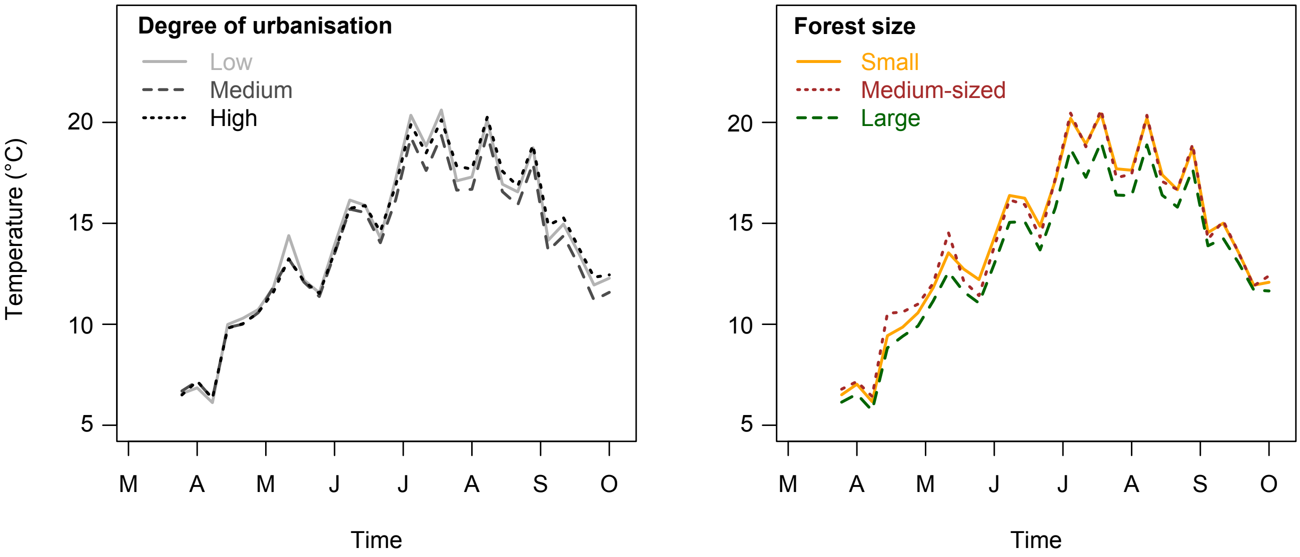


Fig. S2. Decomposition rate of litter (k_{litter}) and lignin (k_{lignin}) plotted against soil moisture content (a, c) and soil pH (b).

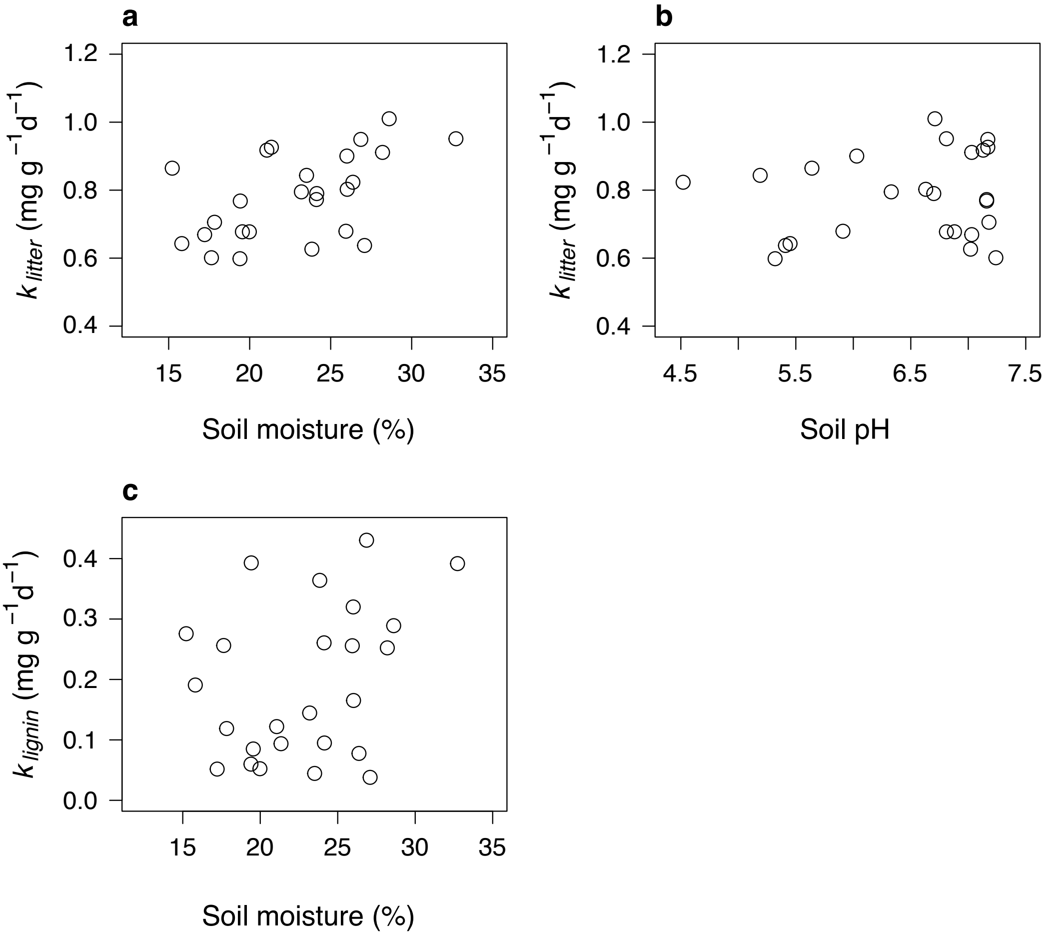
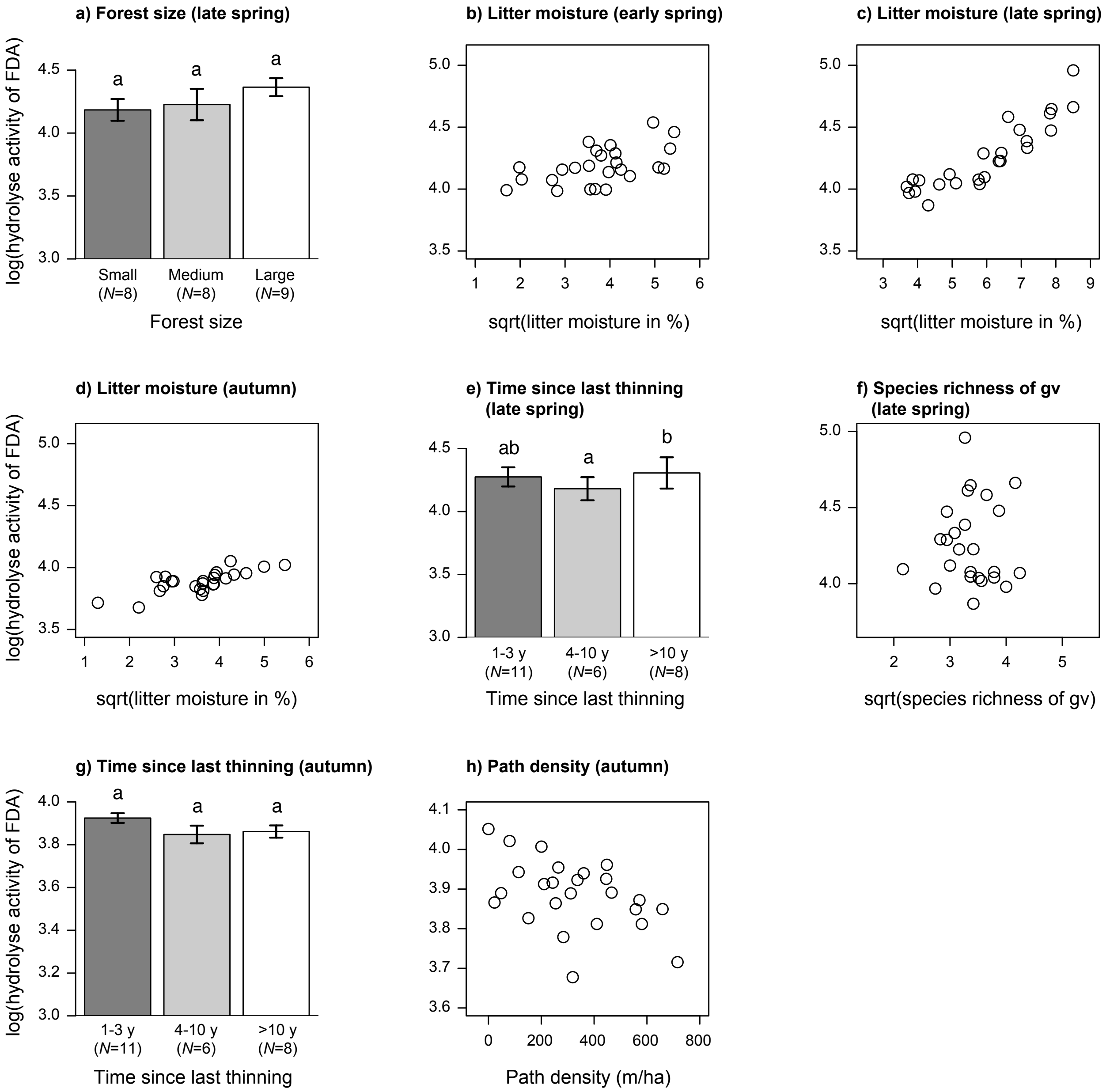


Fig. S3. Microbial activity expressed as the hydrolyse activity of FDA in forests differing in size (a; mean ± SE), moisture content of litter (b, c, d), time since last thinning (e, g; mean ± SE), species richness of ground vegetation (gv; f) and path density (h) at the three sampling dates: early spring (b), late spring (a, c, e, f) and autumn (d, g, h). Different letters next to the bars indicate significant differences among classes. No significant differences were found for the variables not shown.



a) Forest size (late spring)

b) Litter moisture (early spring)

c) Litter moisture (late spring)

d) Litter moisture (autumn)

e) Time since last thinning (late spring)

f) Species richness of gv (late spring)

g) Time since last thinning (autumn)

h) Path density (autumn)

GENERAL DISCUSSION

Urban growth is an important driver of land-use change, which in turn is regarded as a major threat to biodiversity. This is of special importance as it is increasingly rapidly worldwide (Sala et al. 2000; Grimm et al. 2008). This thesis examines the consequences of two underlying drivers of land-use change in urban landscapes – degree of urbanisation and habitat size. Additionally, edge effects are important in urban green areas and their impact may depend on the shape of the habitat remnants and differences between a habitat remnants and its surrounding matrix (Hamberg et al. 2009) – factors that in turn may be influenced by urbanisation. These effects are further enhanced in small sites, which contain higher proportions of edge habitat, than large sites (Matlack 1993). Hence, both changes in the surrounding landscape and habitat size were expected to significantly influence local biodiversity of meadows, ruderal sites and forests as well as decomposition processes of leaf litter in forests.

In the study presented in **Chapter I**, I examined the impact of landscape composition in the closer surroundings and habitat size on the species richness of vascular plants, Orthoptera and Lepidoptera in meadows and ruderal sites. I found that the response of groups of species considerably varied depending on the habitat type, taxonomic group and species trait examined. The species richness of Orthoptera and Lepidoptera was positively related to meadow size but not to the size of ruderal sites, while the opposite was true for plants. The finding in meadows confirms the hypothesis that groups of species at high trophic ranks such as herbivores are more negatively affected by reduced habitat size than plants. The contrasting pattern observed in ruderal sites may be due to the higher disturbance intensity in this habitat type and thus lower competition among plant species. For Lepidoptera in ruderal sites, connectivity expressed as the percentage of ruderal sites in the closer surroundings seemed to be a better predictor of species richness than habitat size per se. I further found that the species richness of both Orthoptera and Lepidoptera decreased with increasing percentage cover of sealed area in the closer surroundings. This negative effect was more pronounced in meadows than in ruderal sites. Surprisingly, plant species richness in both habitat types was not influenced by the percentage cover of sealed area. Linear habitat strips might act as corridors among habitats and thus mitigated isolation effects, even if the percentage cover of these strips is relatively low (Fischer et al. 2006; Tikka et al. 2011). Moreover, plants in ruderal sites were probably better adapted to high levels of disturbances due to their short life cycle and high seed production. These factors, respectively the absence of them, may also be partly responsible for the negative impact of degree of urbanisation on the species richness of forest plants recorded in Chapter II. Important drivers of species composition in meadows were the percentage cover of both sealed area and forest area, and in ruderal sites the percentage cover of other ruderal areas.

Furthermore, the richness of species with particular traits was differently affected by habitat size. In particular, the richness of large-sized species and food specialists of Orthoptera and short-winged species and food generalists of Lepidoptera benefitted from increasing meadow size, while the richness of good dispersers and habitat generalists of Orthoptera increased with the size of ruderal sites. For Lepidoptera, interestingly, I did not detect any species–area relationships for the traits examined in ruderal sites supporting our assumption that species can mitigate potential area effects by acquiring resources from nearby-situated ruderal sites (Dunning et al. 1992; Tscharntke et al. 2002).

In contrast to the two arthropod groups stated above, soil surface-active ants and spiders do not show species-specific mutualistic or exploitative relationships with plants. Similar to Chapter I, **Chapter II** showed that the response of the degree of urbanisation and forest size dependent on the taxonomic group examined. The species richness and diversity of plants were highest in less urbanised areas, while those of ants and spiders did not differ among various degrees of urbanisation. The higher sensitivity of plant species may be explained by differences in mobility of the three focal groups and the high number of food generalists in ants and spiders, which could better cope with the loss of some species at lower trophic rank compared to specialised herbivores and predators (Didham et al. 1996; Holt et al. 1999). Nonetheless, I recorded a more pronounced shift in species composition with increasing degree of urbanisation for ants and spiders at higher trophic rank. In spiders, furthermore, this shift in species composition was accompanied by a slight decrease of functional evenness from less to highly urbanised areas. Regarding forest size, I did not find a species–area relationship for any of the three taxonomic groups examined. However, when I grouped species according to their habitat specificity, a replacement of forest specialists by open-land species with decreasing forest size in both ants and spiders could be observed. In plants, interestingly the shape rather than the size of forests was the main predictor of the percentage of forest specialists. Local site characteristics were also important determinants for species diversity and functional diversity. Abiotic site characteristics were crucial for plant species diversity and species composition, while the structural diversity of both leaf litter and vegetation was important for those of ants and spiders. The findings in **Chapter II** demonstrate that species richness alone is not an ideal indicator of biodiversity change in urban landscapes, as it masked shifts in species composition and relative abundance of species with different habitat specificity and traits.

Finally, the results in **Chapter III** showed that land-use changes associated with urbanisation can also alter important ecosystem functions like leaf litter decomposition processes in forests. In particular, I recorded combined effects of degree of urbanisation and forest size on the decomposition rate of leaf litter (k_{litter}) in the early stage of decomposition. While large forests showed the highest k_{litter} in highly urbanised areas and the lowest in less urbanised areas, the opposite pattern was recorded in small and medium-sized forests. This indicates that abiotic and biotic site characteristics of forests of similar size differently influenced k_{litter} depending on the degree of urbanisation. Hence, decay-promoting factors such as the increased soil temperature and soil pH found in the small and medium-sized forest sites may have counteracted the negative effects of urbanisation, which may have caused the lower k_{litter} values in large forest sites. The enzymatic breakdown of leaf litter mediated by bacteria and fungi plays an important role in the early stage of decomposition (McClaugherty and Berg 2011). In this study, moisture content of litter was the best predictor of microbial activity, followed by forest size. Given that microbial biomass varies greatly both spatially and temporarily at a small scale (McClaugherty and Berg 2011), I suggest that mechanisms associated with degree of urbanisation may be too coarse to detect differences in microbial activity. **Chapter II** and **Chapter III** showed that even small green sites have the potential to make a significant contribution to the conservation of biodiversity and thus important ecosystem functions in cities.

Implications and Outlook

This thesis provides a broad picture of the effects of changing landscape composition and habitat size on the local biodiversity in an urban landscape by giving insights in the response of various groups of species in different habitat types. The findings of this thesis highlight the necessity to consider different taxonomic and functional groups in urban planning to maximise conservation value of urban green areas. In addition to degree of urbanisation, also habitat size was important for the diversity of some groups. This is also interesting, as the sites examined were relatively small, especially when compared to other urban sites in comparable studies. Indeed, urban studies were typically conducted in habitat patches much larger than those in this thesis. It was, therefore, encouraging to find that even small green sites (< 0.1 ha) have the potential to make a significant contribution to biodiversity con-servation and essential ecosystem functions in urban landscapes. Moreover, surveying the literature on the effects of urbanisation on biodiversity in forests revealed that the impact of urbanisation on the diversity of soil detritivores – a potential prey for soil-surface active arthropods and an important component of leaf litter decomposition – is poorly understood and needs further investigations.

The findings of this thesis have several implications for the management of green areas in the city of Basel and its suburban surroundings. Conservation measures in urban areas mainly focus on semi-natural habitats such as meadows and forests, while ruderal sites are frequently neglected (Muratet et al. 2007; Knapp et al. 2008). However, the fact that taxonomic groups in ruderal sites responded differently to the urbanisation-related factors examined than those in meadows highlights the importance of developing habitat-specific conservation plans. Furthermore, I recommend that urban planners develop more flexible management strategies to satisfy the different requirements of various groups of species. In the short term, urban planners could focus on small-scale environmental factors, which proved to be important determinants of species diversity and species composition – in particular for species at higher trophic ranks and habitat specialists (Chapter II). For example, the protection of litter layers and ground vegetation in forests could be enhanced using simple management practices. As primary products enter food webs in forests mainly as dead organic matter (Swift et al. 1979; Cebrian and Lartigue 2004), locally adjusted management practices to sustain decomposition processes may also be beneficial for species at higher trophic rank and thus ensure the functioning of other ecosystem services. In meadows, extensive and step-wise mowing as well as leaving grass stripes in place over winter can enhance reproduction and overwintering success in various groups of arthropods. This thesis, moreover, showed that the composition of the surrounding landscape plays an important role for species' persistence in urban landscapes, because it can mitigate or intensify the consequences of habitat loss and spatial isolation (Godefroid and Koedam 2007; Sattler et al. 2010; Vallet et al. 2010). The influence of large-scale factors including the proportion of sealed area and forest size on forest specialists in Chapter II indicates that also more complex changes at the landscape level are required to maintain vulnerable elements of species communities. This can be achieved, for example, by enhancing the quality of other green sites surrounding the target habitats or creating linear habitat stripes and disruptions within the built component (e.g. vegetated walls or roofs, Lundholm 2006; Lizée et al. 2012) to enhance movement of species. These management actions can substantially contribute to counteract the negative consequences of urban sprawl and densification on biodiversity.

References

Cebrian J., Lartigue J., 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol. Monogr. 7: 237–259.

Didham R.K., Ghazoul J., Stork N.E., Davis A.J., 1996. Insects in fragmented forests: a functional approach. Trends Ecol. Evol. 11: 255–260.

Dunning J.B., Danielson B.J., Pulliam H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Fischer J., Lindenmayer D.B., Manning A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4: 80–86.

Godefroid S., Koedam N. 2007. Urban plant species patterns are highly driven by density and function of built-up areas. – Landscape Ecol. 22: 1227–1239.

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.

Hamberg L., Lehvävirta S., Kotze D.J., 2009. Forest edge structure as a shaping factor of understorey vegetation in urban forests in Finland. Forest Ecol. Manag. 257: 712–722.

Holt R.D., Lawton J.H., Polis G.A., Martinez N.D., 1999. Trophic rank and the species–area relationship. Ecology 80: 1495–1504.

Knapp S., Kühn I., Mosbrugger V., Klotz S., 2008. Do protected areas in urban and rural landscapes differ in species diversity? Biodiver. Conserv. 17: 1595–1612.

Lizée M.H., Manel S., Mauffrey J.F., Tatoni T., Deschamps-Cottin M., 2012. Matrix configuration and patch isolation influences override the species–area relationship for urban butterfly communities. Landscape Ecol. 27: 159–169.

Lundholm J.T., 2006. Green roofs and facades: a habitat template approach. Urban Habitats 4: 87–101.

Matlack G.R., 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. Biol. Conserv. 66: 185–194.

McClaugherty C.A., Berg B., 2011. Soils and decomposition. eLS.

Muratet A., Machon N., Jiguet F., Moret J., Porcher E., 2007. The role of urban structures in the distribution of wasteland flora in the greater Paris area, France. Ecosystems 10: 661–671.

Rebele F., 1994. Urban ecology and special features of urban ecosystems. Glob. Ecol. Biogeogr. 4: 173–187.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M., Wall D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Sattler T., Duelli P., Obrist M.K., Arlettaz R., Moretti M., 2010. Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecol. 25: 941–954 .

Swift M.J., Heal O.W., Anderson J.M., 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, CA.

Tikka P.M., Högmander H., Koski P.S., 2001. Road and railway verges serve as dispersal corridors for grassland plants. Landscape Ecol. 16: 659–666.

Tscharntke T., Steffan-Dewenter I., Kruess A., Thies C., 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecol. Res. 17: 229–239.

Vallet J., Beaujouan V., Pithon J., Rozé F., Daniel H., 2010. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. Biodivers. Conserv. 19: 3375–3392.