

**The impacts of urbanisation and forest size on  
antagonistic ecological interactions and forest  
ecosystem services**

**Inauguraldissertation**

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

Philosophisch-Naturwissenschaftlichen Fakultät  
der Universität Basel

von

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Basel, 2021

Originaldokument gespeichert auf dem Dokumentenserver der Universität  
Basel

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Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät  
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Basel, den 13. Oktober 2020

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## **ACKNOWLEDGEMENTS**

Naturally, I would like to thank Prof. Bruno Baur for his considerate, straightforward, and effective guidance. His thoughtful, fast, and concise feedback helped drive this thesis to completion.

Secondly, I would like to thank my supervisor Hans-Peter Rusterholz for his comprehensive support and enduring patience. I thank him for various scientific methodologies he introduced me to and assisting me with the statistical analyses. I would like to in particular thank him for the time-consuming third project, in which he assisted me greatly in extraction of fungal DNA from deadwood (Chapter III).

I would also like to thank Evelyn Meyer for the help with the administrative work. Thank you to Brigitte Braschler for reading through the manuscripts and together with Txomin Gilgado for engaging and interesting entomological discussions. Additionally, I would like to thank former PhD students Luca Gaggini and Ramona Melliger for their helpful advice and answers about any queries I had. Thank you also to Jon Andreja Nuotclà, Raquel Lázaro Martín, Benjamin Eggs, Elena Haeler, and Thibault Lachat for helpful advice.

I would like to thank various entomological experts that identified part of the arthropods I collected during my thesis. So, a thank you to Jörg-Alfred Salamon for identifying the Acari and Collembola in the litter decomposition project (Chapter II). A thank you to Manfred Ulitzka for identifying the Thysanoptera and Benedikt Feldmann for identifying the Staphylinidae for the saproxylic fauna project (Chapter III). Not to forget the various entomological experts that were kind enough to provide me support and verify my insect identifications. So, thanks to Marcela Skuhrová for the gall midges, Richard Askew for the parasitoids of gallers, Christoph Germann for verifying just the third find in Switzerland of an exotic weevil, and Paul Beuk for the Diptera.

Next I would like to thank my work colleagues at the NLU for a pleasant work environment. Added to that I would like to thank two helpers Denise Binggeli for litterbag preparation and Roman Schneider for help with distributing and tying the deadwood branches on trees amongst the forests of Basel.

I would like to thank the various foresters of Baselstadt and Baselland, Stadtgärtnerei Basel, Christoph Merian Stiftung, and the private landowners for access to the forest sites. In particular I would like to thank the foresters Adrian Amsler and Markus Lack of Allschwil for providing the fresh deadwood and allowing me to use their wood shack for my emergence traps (Chapter III).

Financial support was received from Emilia Guggenheim-Schnurr Stiftung, Basler Stiftung für biologische Forschung, and Basler Stiftung für experimentelle Zoologie.

## *Acknowledgements*

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Lastly I would like to thank my family for their patience and support like spending New Years building the wooden shelves for the emergence traps, and of course the countless fruits from the garden and cakes that nourished me through the years of my thesis.

# **CONTENTS**

Summary .....	3
General Introduction .....	7
Chapter I: Urbanisation and forest size affect the infestation rates of plant-galling arthropods and damage by herbivorous insects .....	15
Chapter II: Leaf litter decomposition and litter fauna in urban forests: Effect of the degree of urbanisation and forest size .....	31
Chapter III: Saprophytic insects and fungi in deciduous forests along a rural-urban gradient .....	75
General Discussion .....	115



## **SUMMARY**

One of the main human-induced changes to the natural environment is the rapid expansion of urban areas throughout the world. Urbanisation can lead to a reduction of habitat sizes and increased spatial isolation of the remaining green areas. In European cities, forests are the most frequent type of urban green areas. Forests do not only provide air filtration, recreation and psychological benefits for the human citizens, but also constitute a habitat for a variety of organisms. These green areas are subjected to urbanisation-associated abiotic changes such as increased temperature. These environmental changes can affect the composition of plants and their nutritional quality, which in turn can influence other antagonistic and beneficial trophic levels dependent on living tissues (herbivores) and dead plant matter (decomposers). In my thesis, I investigated the effects of urbanisation and forest size on several groups of arthropods with a variety of ecological functions.

In the first study, the aim was to evaluate whether plant-galling infestation rates and leaf damage by mining and chewing arthropods on three common tree species (sycamore, beech, and ash) are influenced by the degree of urbanisation and forest size. For this purpose, I assessed the frequencies of gall infestation and leaf damage in 20 forests in the city of Basel and its surroundings. There were contrasting responses among the plants and herbivorous arthropods investigated. Total galling infestation rates on sycamore and infestation rates of beech gall midges were highest in forests situated in low urbanised areas, whereas only beech gall midges had a clear negative response to decreasing forest size. Regarding the herbivorous arthropods on sycamore, the total leaf area damage by mining and chewing arthropods was influenced by urbanisation and also increased with increasing forest size. Leaf miners on beech leaves tended to be affected by degree of urbanisation.

The leaf litter decomposition process is vital for nutrient recycling and uptake of nutrients for plants in forests. In the second study, the aim was to examine whether litter decomposition rates and the associated mesofauna are influenced by the degree of urbanisation and forest size. To assess the rate of leaf litter decomposition in urban and sub-urban areas of Basel, I used standardised litterbags with three different mesh sizes filled with a mixture of leaves of three common tree species (sycamore, beech and ash) that differ in their natural rate of decay. Litterbags were exposed for 3, 6 or 9 months in 17 forests. The leaf litter decomposition rate was negatively affected by the degree of urbanisation, while forest size had no significant influence. The mesofauna (consisting mainly of Acari and Collembola) contributes to the process of leaf litter decomposition. Therefore I also examined how the mesofauna in the litterbags responded to urbanisation and forest size. The mesofauna showed contrasting responses to urbanisation. The oribatid mites (Acari) were most abundant in forests in

moderately urbanised areas, while Collembola were more most abundant in forests situated in highly urbanised areas. Furthermore, forest size influenced the mesofauna. Medium-sized forests had the lowest abundances of Acari and large forests the highest abundance of Collembola. There was, however, no shift in Collembola species composition in response to urbanisation. Nevertheless, urbanisation affected Collembola species with specific traits. Collembolans with a globular body shape were most abundant in forests of medium-size and situated in low urbanised areas, and the eudaphic (mainly soil-living) collembolans tended to be less abundant in small forests.

Deadwood is an integral component of forests in terms of nutrient recycling, forest regeneration, water retention, and also provides an essential habitat for nearly a quarter of the forest arthropod species. In the third study, the aim was to investigate factors that influence the deadwood-dependent (saproxylic) insect and fungal communities along a rural-urban gradient. I exposed freshly cut beech and oak branches as bait for saproxylic insects and fungi in 25 forests situated in Basel-city and its surroundings for 8 months to examine effects of landscape factors (degree of urbanisation), local factors (forest characteristics such as tree species composition at the forest site and volume of naturally occurring deadwood) and branch characteristics (e.g. moisture content of branch deadwood) on the saproxylic community. I also used subsamples of drilling chips from each branch to determine fungal species richness (operational taxonomic units OTUs) and abundance using a molecular technique. Altogether more than 193,500 insects emerged from the branches and were identified to the lowest possible taxonomical level. Urbanisation reduced the number of total saproxylic insects, bark beetles, longhorn beetles, flies, moths and ichneumonid wasps. Species richness of saproxylic insects was not affected by the degree of urbanisation or any forest characteristic. In contrast, total insect taxonomic composition was altered by wood moisture content (a branch characteristic) and the beetle species composition shifted with the degree of urbanisation and pH of branch wood. In saproxylic fungi, the total number of OTUs decreased with increasing degree of urbanisation. The total number of fungal OTUs was also positively influenced by the volume of naturally occurring fine woody debris at the forest site. The composition of fungal OTUs was affected by the degree of urbanisation and wood pH. These detected shifts in the composition of both saproxlic insects and fungi result in alterations in the associations between saproxylic insects and fungi along the rural-urban gradient.

In my thesis I was able to demonstrate that urbanisation has the potential to disrupt interactions between arthropod and living as well as dead plants (litter and wood). The difference in responses to urbanisation by the variety of arthropods investigated indicates that taxonomical differences can respond contrastingly to the same urban pressure. This is a result of differences in life-history and morphological traits, resource availability, and sensitivities

to the altered micro-climatic conditions within urban areas. The changes in species composition in some arthropod groups (e.g. saproxylic insects and fungi) show that urbanisation can filter for certain species better adapted to the urban environment. This might not only lead to reductions in the abundance or even species richness of insects, but also reduce the efficiency in ecosystem services of urban forests such as litter and deadwood decomposition.



## **GENERAL INTRODUCTION**

Large-scale land-use changes induced by humans have occurred in Europe for centuries (Kaplan et al. 2009). In the past decades (since the 1950s), urbanisation is becoming more and more a main driver of land-use change (Fuchs et al. 2013). In fact, between 1950 and 2010, urban areas in Europe increased by almost 25% (35,818 km<sup>2</sup>; Fuchs et al. 2013). The ongoing increase in the human population worldwide (UN Urban Agenda 2016) will further increase the area covered by cities. Urban areas are heterogeneous landscapes consisting of sealed areas with a mosaic of green areas (e.g. ruderal areas, grasslands, meadows, parks, gardens, and forests), buildings and traffic infrastructure. Habitats within the urban environment are often characterised by a high temperature (known as the urban heat island effect), increased nitrogen deposition and soil compaction, and high frequency of disturbances (Grimm et al. 2008; Pickett et al. 2011). Urbanisation-induced fragmentation of the remaining semi-natural habitats such as forests lead to a reduction in habitat size and spatially isolated plant and animal populations (New 2015; Lepczyk et al. 2017).

Nevertheless, urban habitats can provide a wide variety of ecosystem services for the residents including physiological and psychological benefits for citizens (Clark et al. 2014), areas for recreation, recycling and storage of nutrients, air filtering and temperature regulation as well as habitat for plant and animal species (Ives et al. 2016).

The quality of a habitat patch, its size, and the type of the surrounding landscape (matrix) are important factors determining the species composition of plant and animal communities (Prevedello and Vieira 2010; Williams and Winfree 2013; Beninde et al. 2015; Lepczyk et al. 2017). Urbanisation creates novel habitats (Kowarik 2011), which promote thermophilous species as shown in spiders (Horváth et al. 2012) and staphylinid beetles (Magura et al. 2013). Furthermore, urbanisation can push the evolution of ecophysiological changes for a higher temperature tolerance as found in ants (Angilletta et al. 2007). On the other hand, urbanisation can negatively impact forest specialists (Sadler et al. 2006; Magura et al. 2013). Urbanisation-induced environmental changes and fragmentation of habitats can lead to lower functional diversity and biotic homogenisation. In arthropods, urbanisation-related selection favours diet generalist and highly mobile, thermophilous species (butterflies: Merckx and Dyck 2019; carabid beetles: Piano et al. 2017).

Arthropods are one of the most diverse groups of living organisms and inhabit a wide array of niches and habitats (Grimaldi and Engel 2005). Due to their high abundance and diversity, terrestrial arthropods provide vital ecosystem services such as pollination, natural enemy pest control, nutrient recycling and decomposition (Losey and Vaughan 2006). Many arthropods have short generation times and thus are able to respond rapidly to anthropogenic

changes to natural habitats. Arthropods are therefore suitable indicators for the assessment of environmental changes (Kremen et al. 1993; McGeoch 1998; Uehara-Prado et al. 2009). In recent years, there is an increased research effort examining the responses of various arthropod groups to urbanisation (Raupp et al. 2010; New 2015; Fenoglio et al. 2020), and on the ecosystems services the arthropods provide (Shochat et al. 2006; Turrini et al. 2016).

### **Focus of the thesis**

My PhD-thesis consists of three separate studies. The main goal of the thesis was to investigate the effects urbanisation and forest size on various arthropod groups in Basel-Stadt and its rural surroundings, Switzerland. The studies were carried out in forests varying in sizes and embedded in the urban or rural matrix, constituting a rural–urban gradient. The degree of urbanisation was determined by the percentage of sealed area within a radius of 500 m around the investigation area.

The effects of increasing degree of urbanisation can have varying outcomes in terms of herbivory rates, abundances and species richness of arthropods. Some studies found clear negative effects on abundances and species richness of arthropods (McKinney 2008; Niemelä and Kotze 2009; Ramírez-Restrepo and MacGregor-Fors 2017), and herbivory rates (Moreira et al. 2019). Others found no effects of urbanisation on arthropod abundances, richness and herbivory rates (Fenoglio and Salvo 2010; Rossetti et al. 2017). In some cases, certain arthropods have higher abundances in highly urbanised areas than in rural ones (Meineke et al. 2013). Because of the different responses of arthropod species to urbanisation, it is important to investigate a broad range of organisms to get a better understanding of how anthropogenic habitat changes can impact animal populations and ecosystem services (e.g. litter and deadwood decomposition) and disservices (herbivory) they provide.

In **Chapter I**, I focused on herbivorous arthropods including a specialised form of herbivory known as galling. A gall is created by antagonistic stimuli of feeding and injecting growth hormones by the herbivore and the defensive response of the plant to “close/protect” the wound, which in turn results in encapsulating the herbivore within spherical, conical plant structures (Ananthakrishnan 1984; Redfern et al. 2011). These arthropods are ideal to examine both urbanisation-related effects of environmental changes and the effect of forest size, because the majority of galling arthropods are oligophagous or monophagous (Fernandes et al. 2014), and thus are bound to the availability and quality of their host plants (Cornelissen et al. 2008). To assess the gall infestation and herbivory rates on three common tree species (sycamore, beech and ash), I conducted field surveys at the edges and interior of 20 deciduous forests in Basel and its surroundings. Galling, mining and chewing herbivorous arthropods often differ in life-history traits and thus may respond to urbanisation, habitat size and the surrounding landscape (degree of urbanisation) in different ways.

In **Chapter II**, I focused on an important ecosystem service of forests, namely leaf litter decomposition. The decomposition of leaf litter is vital for the formation of soil and the recycling of nutrients to make it accessible for uptake for plants (Berg and McClaugherty 2014). The process of litter decomposition is governed by the mechanical degradation of macro-organisms (body size >2 mm such as earthworms and snails), then further degraded by meso-organisms (200 µm–2 mm such as mites and springtails) to be finally processed by micro-organisms (<100 µm; mainly fungi and bacteria; Bradford et al. 2002). To assess the potential effects of urbanisation and forest size on litter decomposition, I exposed standardised litterbags filled with litter of three common tree species that exhibit varying decay rates. I used litterbags with three different mesh sizes to exclude litter organisms of different size and examine whether these exclusions impacted the litter decomposition rates. Furthermore, I assessed whether urbanisation, forest size and local habitat factors influence the abundance of the ground-dwelling litter mesofauna, species richness, species composition, and traits exhibited by the different species.

In **Chapter III**, I turned my attention to deadwood-dependent (saproxylic) insects and fungi. It has been estimated that up to 20% of the organisms within northern European forests are dependent on deadwood at some stage of their life cycle (Stokland et al. 2012). Therefore, the abundances and diversity of saproxylic organisms can be used as a proxy for the biodiversity of a forest (Stokland et al. 2012). In the past centuries, ecological degradation of forests in central and western Europe through an increased management (logging) intensity had a negative impact on the diversity of saproxylic beetles (Müller and Bütler 2010; Seibold et al. 2015) and fungi (Müller et al. 2007; Purahong et al. 2014). Saproxylic beetles have been extensively studied. However, other saproxylic insects including flies, moths and parasitic wasps have received little attention. Within an urban context, saproxylics have only been touched upon and studies often only focused on one family of beetles (Fattorini and Galassi 2016), one ecological niche (tree hollows; Peuhu et al. 2019) or on one locality (i.e. a single park; Graf 2012). Apart from one study in Belgium (Piel et al. 2005) on the spruce bark beetle (*Ips typographus*), there exists no study to date that investigated the effects of degree of urbanisation on saproxylics. So, I used an experimental approach and exposed in a standardised way freshly cut oak and beech branches as deadwood bait for saproxylics in 25 forests along a rural-urban gradient in Basel and its surroundings for 8 months. The emerged saproxylic arthropods (altogether more than 193,500 individuals) were identified and their abundances, species richness and taxonomic composition were evaluated in relation to the degree of urbanisation and landscape and local factors. I also used subsamples of drilling chips from each branch to determine fungal species richness (operational taxonomic units OTUs) and abundance using a molecular technique. Then I examined the fungal diversity and

composition and evaluated whether associations between saproxylic insects and fungi were altered by urbanisation.

In the **General Discussion** I discuss the most important findings of my three projects and present potential implications on arthropods in forests along a rural-urban gradient.

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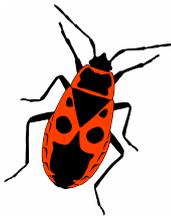
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## **Chapter I**

### **Urbanisation and forest size affect the infestation rates of plant-galling arthropods and damage by herbivorous insects**

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*European Journal of Entomology*, 2020, 117: 34–48



## Urbanisation and forest size affect the infestation rates of plant-galling arthropods and damage by herbivorous insects

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**Key words.** Urbanisation, forest size, arthropods, insects, herbivory, galls, parasitoid, chewing, mining

**Abstract.** Urbanisation is increasing globally and is considered to be a main driver of environmental change. Urbanisation-related factors include reduced habitat size and increased spatial isolation of the remaining habitats. As a consequence, the dynamics of plant and animal populations may change, which in turn might influence the quality and quantity of plant resources. Thus, urbanisation has the potential to disturb plant-animal interactions such as herbivory or galling. In the urban-rural setting of Basel (Switzerland), we aimed to assess whether the degree of urbanisation and forest size influence plant-galling infestation rates and leaf damage by mining and chewing arthropods on three tree species (sycamore, beech, and ash). We recorded species-specific responses to the degree of urbanisation and forest size. Gall infestation rate on sycamore leaves was affected by urbanisation but not by forest size. In contrast, gall infestation rates of beech gall midges responded sensitively to increasing urbanisation and decreasing forest size. The total leaf area damage caused by mining and chewing arthropods on sycamore was influenced by urbanisation and increased with increasing forest size. Leaf area damage by miners in beech tended to be affected by the degree of urbanisation, but not in ash. Urbanisation and forest size have the potential to alter herbivorous insect abundances. However, the effects depend on tree species and herbivore guild.

### INTRODUCTION

Urbanisation is increasing globally with a projected population growth of 2.5 billion people in urban areas by 2050 (UN Urban Agenda, 2016). Urbanisation is therefore considered a major driver of environmental change (Marzluff et al., 2008; Groffman et al., 2014). The expansion of built-up areas reduces the size of natural habitat patches, increases the spatial isolation of the remaining patches and alters the environmental conditions (New, 2015). Studies along urbanisation gradients have shown increases in temperature (e.g. heat island effect) and nitrogen deposition and decreases in precipitation from rural surroundings to the city centre (McIntyre, 2000; Pickett et al., 2011). These environmental changes may influence habitat quality (McKinney, 2008) and thus alter plant species richness and composition (Schmidt et al., 2014). Furthermore, these urbanisation-related changes in environmental factors can potentially affect both the quantity (primary production) and quality (chemical composition) of the plants occurring in the habitat patches (McKinney, 2008), which in turn may influence higher trophic levels. Correspondingly, several studies revealed that urbanisation reduces species richness and changes the species composition of invertebrates (McKinney, 2008; McDonnell & Hahs, 2015). Urbanisation-related decreases in species richness were reported

in butterflies (Di Mauro et al., 2007). Martinson & Raupp (2013) reported a decrease in species richness in carabid beetles, particularly in large, predatory and poor dispersing species and those that have strict habitat requirements. However, in the same meta-analysis, Martinson & Raupp (2013) reported an overall neutral effect of urbanisation on coleopteran herbivores, but a negative effect on the tiny herbivores in this insect order. In contrast, several studies showed that urbanisation increased the abundances and infestation rates of herbivorous arthropods (Christie & Hochuli, 2005; Raupp et al., 2010).

A major aspect of urbanisation is the fragmentation of natural and semi-natural habitats (Marzluff et al., 2008; Raupp et al., 2010). Some meta-analyses reveal an overall lower level of damage by herbivorous insects in fragments (Martinson & Fagan, 2014), whereas others reported a neutral effect on overall herbivory (Rossetti et al. 2017). Fragmented forests also seem to be subjected to more pronounced edge effects than other semi-natural habitats (Marzluff et al., 2008; Dale & Frank 2014). This assumption was confirmed by several studies, which reported both a higher abundance and species richness of herbivorous arthropods and thus a higher extent of leaf damage in forest edges than in the forest interior (Christie & Hochuli, 2005; Guimarães et al., 2014).

Plant-arthropod interactions are important for the structure of ecosystems, because arthropods are the most diverse and abundant plant consumers and are important prey items (McIntyre, 2000; Faeth et al., 2005; Raupp et al., 2010). Plant-galling arthropods are a good model system for assessing the response to environmental changes because of their sedentary nature and high plant host specificity (Fernandes et al., 2014), and thus are dependent on plant host quantity and quality (Cornelissen et al., 2008). A variety of organisms can induce galls, including mites, aphids, wasps and midges (Redfern et al., 2011). Galls are induced by the stimuli of feeding and/or the release of growth hormones by both the arthropod that initiates the gall and subsequently the larvae developing within the gall interacting with the defensive response of the host plant (Ananthkrishnan, 1984). Galling organisms can alter plant phenology and enhance plant quality, which can benefit other herbivorous arthropods (Ohgushi, 2005; Cornelissen et al., 2016). Plant-galling arthropods are able to create an optimal micro-climate inside their galls allowing them to regulate the humidity (Price et al., 1987; Miller III et al., 2009) and are therefore highly successful and diverse in dry environments (Fernandes & Price, 1992). The few studies investigating the impact of urbanisation on the infestation rates of the plant-galling arthropods yielded contrasting results. McGeoch & Chown (1997) and Mingaleva et al. (2011) reported a reduction in infestation rates of galling arthropods with urbanisation, whereas Dreistadt et al. (1990) and Sumoski et al. (2009) reported positive effects and Skrzypeczyńska (2004) found an overall neutral effect of urbanisation.

Forests are one of the most frequent types of green area in cities and provide a wide range of ecosystem functions (Dwyer et al., 1992). We examined the impacts of degree of urbanisation and forest size on the occurrence and frequency of plant-galling arthropods and the extent of leaf damage by other herbivorous insects on three tree species (*Acer pseudoplatanus*, *Fagus sylvatica* and *Fraxinus excelsior*) in the city of Basel, Switzerland. In particular, we examined the following question: Are the infestation rates of galls and extent of grazing damage to leaves on young sycamore, beech and ash trees differently influenced by both the degree of urbanisation and size of urban forests?

## MATERIALS AND METHODS

### Study area

This study was carried out in the Canton of Basel-Stadt, Switzerland (hereafter referred to as Basel, 47°34'N, 7°36'E, elevation: 245–522 m a.s.l.). The area studied is 37 km<sup>2</sup>, consisting of a residential area of 26.3 km<sup>2</sup> (70.9%), 4.5 km<sup>2</sup> of agricultural land (12.1%), 4.4 km<sup>2</sup> of forest (11.7%) and 1.7 km<sup>2</sup> of water bodies (4.5%). It includes the city of Basel and the municipalities Riehen and Bettingen with a total of 198,206 citizens. Basel has a mean annual precipitation of 842 mm and mean annual temperature of 10.5°C.

### Forest and landscape characteristics

To assess the potential effects of the degree of urbanisation and forest area on the diversity of plant galls, we chose 20 mixed deciduous forests ranging in size from 258 m<sup>2</sup> to 50,000 m<sup>2</sup> (Table

S1). These forests are embedded in a small-scale mosaic of settlements and green areas with different habitats within short distances. Historically, these forests were either part of larger forests or planted in the 19<sup>th</sup> century (Table S1). Management of the forests (time since last thinning and management intensity) did not differ between the forests investigated. In these forests, the target tree species: sycamore (*A. pseudoplatanus*), European beech (*F. sylvatica*) and ash (*F. excelsior*), are the most abundant species in both the tree and shrub layer. A high richness of vernal geophytes including *Anemone nemorosa*, *Ranunculus ficaria*, *Polygonatum multiflorum* and *Arum maculatum* occurs in the ground vegetation. Plant species richness and composition of the ground vegetation and in both the shrub and tree layers were determined in each forest (Melliger et al., 2017). Canopy closure was assessed using twelve photographs of each forest, which were then analysed using the pixel counting function in Adobe Photoshop (version 10.0.1). In addition, potential effects of soil characteristics on plant galls and gall infestation rates, soil moisture content (%), total soil organic matter content (SOM) and total soil organic nitrogen were determined for each forest (Melliger et al., 2017).

To assess the degree of urbanisation, the percentage cover of sealed area within a radius of 500 m around the study site in each forest was determined using satellite images of each forest (Google Earth, 2009, date: 6 May 2014) and pixel counting function in Adobe Photoshop (version 10.0.1). The degree of urbanisation of the 20 forests examined ranged from 3% to 70% (Table S1).

### Plant gall survey

In each forest, we established six sampling plots measuring 2 m × 2 m. Three of them were randomly placed at the forest edge and three in the forest interior (at least 5 m from the forest edge). The only criteria were that at least one of the three tree species had to occur in each plot. The inter-plot distance always exceeded 5 m. In each plot, we recorded the number of young trees (height: 30–250 cm) of three species: sycamore (*A. pseudoplatanus*), European beech (*F. sylvatica*) and European ash (*F. excelsior*). On each of these trees, we counted the number of uninfested and gall-infested leaves. Furthermore, we measured the height of each tree in each plot. Tree density was expressed as the number of trees per 4 m<sup>2</sup> for each species in each plot. Overall, we surveyed a total of 804 trees and 41,557 leaves; 328 sycamore trees (8,276 leaves), 315 beech trees (29,403 leaves) and 161 ash trees (3,878 leaves) in the 20 forest sites.

The galls were identified to species level using the keys of Buhr (1964/65), Redfern et al. (2011) and Bellmann (2012), with a few exceptions. *Aceria cephalonea* and *Aceria macrorhyncha* were grouped together as sycamore gall mites, while the aphid *Prociophilus* and the psyllids of the genus *Psyllopsis* were identified to genus level. The plant gall survey was conducted between 16 August and 7 September 2016.

### Gall mortality

We determined the percentage of mortality of galling arthropods in a sub-sample of the infested leaves recorded for each tree species in each plot. We randomly selected six leaves from each focal tree species among all leaves infested by galls in each plot. The sampling procedure yielded 533 leaves (204 sycamore, 238 beech and 91 ash leaves) with a total of 1,099 individual galls. 863 plant galls (excluding 126 gall mite galls, 6 aphid galls and 104 psyllid galls because of the uncertainty of the identification of the inhabitants) were dissected and gall mortality type was determined according to the modified key of Kelch et al. (2016). We classified mortality as: parasitoid attack, predation, fungus infection or unknown. The classification “unknown” was given to fully

formed galls with no inhabitant (larvae or pupae) present. Larvae and parasitoids in the plant galls were identified using the Universal Chalcidoidea Database (Noyes, 2012) and Himenoptera de Ponent (Escolà, 2012) and the parasitoid larval key in Redfern & Askew (1992).

### Leaf damage

Damage of leaves by herbivores was expressed as percentage leaf area lost and was considered as a measure of the herbivore pressure in urban forests. We randomly sampled six leaves from each focal tree species in each plot between 16 August and 7 September 2016. When there were more than six young trees (height: 30–250 cm) of a particular species in a plot we randomly chose six trees and sampled a single leaf from each tree. The six leaves covered the height range of 30 to 250 cm. When less than six young trees of a species were present in a plot (mainly ash), then we sampled two or more leaves from each tree over the entire height range. To determine the percentage leaf area removed by arthropod feeding, we used the WinDias 3.03 Image Analysis System (Delta-T Devices Ltd., UK). Leaf damage was then categorized into three types using a slightly modified classification of Gossner et al. (2014): (1) chewing damage such as circular area of damage, for example caused by adult beetles of *Orchestes fagi* in spring on *F. sylvatica* leaves, and chewing of leaf margins caused by larvae of various Lepidoptera, Symphyta and Coleoptera, or (2) damage caused by leaf mining moths and beetles. To identify the species that caused the leaf damage we used the key provided by Gossner et al. (2014) and the website <http://bladmineerders.nl/> as an identification guide (Ellis, 2017).

### Statistical analyses

Data analyses for each tree species were conducted separately, because beech trees did not occur in some forests. The infestation rates of plant galls was assessed at the leaf level for each of the three tree species. The percentage infestation by plant galls was calculated using the number of leaves infested divided by the total number of leaves in each plot. The infestation rate was calculated for all galls combined and for those induced by the following species: *Aceria* spp., *Pediaspis aceris*, *Mikiola fagi*, *Hartigiola annulipes*, and *Psylloopsis* sp., separately. The gall-ing-arthropods *Dasineura fraxini* and *Prociphilus* sp. were only recorded in a few forests and therefore could not be considered in further analyses. The percentage of leaves damaged was first based on the number of leaves, which exhibited any sign of damage (e.g. chewing damage) divided by the total number of leaves examined. In a second approach, each leaf sampled from the three tree species was assessed for leaf damage (expressed as percentage of total area damaged). In addition, the percentage of area damaged by chewing and mining arthropods or by fungi was also determined. For data analysis, mean values were calculated for the different plant galls and leaf damage data for each of the tree species for each plot. Leaf damage caused by herbivorous arthropods, which were recorded in less than half of the forests, were omitted from this analysis.

Based on the percentage of cover of sealed area in their surroundings, the forests were classified into sites with low (<15%), medium (15–30%) or high (>30%) degree of urbanisation. Forests were also assigned to one of three size classes: small (<4,000 m<sup>2</sup>), medium-sized (4,000–10,000 m<sup>2</sup>) or large (>10,000 m<sup>2</sup>) forests (Table S1). Preliminary analyses revealed that the edge factor had no effect on the overall gall infestation rate in any of the three tree species or for any of the galling arthropod species separately. Neither was there an effect on the different types of leaf damages. We therefore analysed the mean values of the data of the six plots in each forest without considering the edge factor.

We used analysis of covariance (ANCOVA) to examine potential effects of the degree of urbanisation and forest size on the infestation rate of leaves by each plant gall species separately as well as all species of galling insects combined. We used degree of urbanisation and forest size as factors, and various forests characteristics as cofactors in the ANCOVA models for all three tree species. First, we tested for inter-correlation among the explanatory variables (Table S2a–f). Variables that were not normally distributed were transformed (arcsin sqrt). Percentage of sycamore leaves infested with the galls of *Aceria* spp. and *Pediaspis aceris*, percentage sycamore leaf area damage caused by chewing and mining insects and damage by *Heterarthrus aceris*, *Heterarthrus cuneifrons* and *Stigmella speciosa* were transformed. For beech, percentage leaf area damage by mining and by *Orchestes fagi* and for ash total percentage leaf area damage and percentage of damage due to mining insects and *Gracillaria syringella* were transformed. We checked the residuals of the ANCOVA for normal distribution using Shapiro-Wilk Normality test. The results indicated that the requirements of the model were fulfilled. The same model was used to assess the influence of the degree of urbanisation and forest size on the percentage of leaf area damaged by herbivorous arthropods and endophytic fungi. Furthermore, five frequently occurring species of galling insects and five herbivorous species were statistically analysed.

All models were stepwise reduced as recommended in Chapter 9 Statistical Modelling by Crawley (2007), but the main factors, degree of urbanisation and forest size, were always retained. We used the *Tukey HSD* function for multiple comparisons (post hoc tests) between the different classes of degree of urbanisation and forest size. Statistical analyses were performed using software R (R Core Team, 2015).

## RESULTS

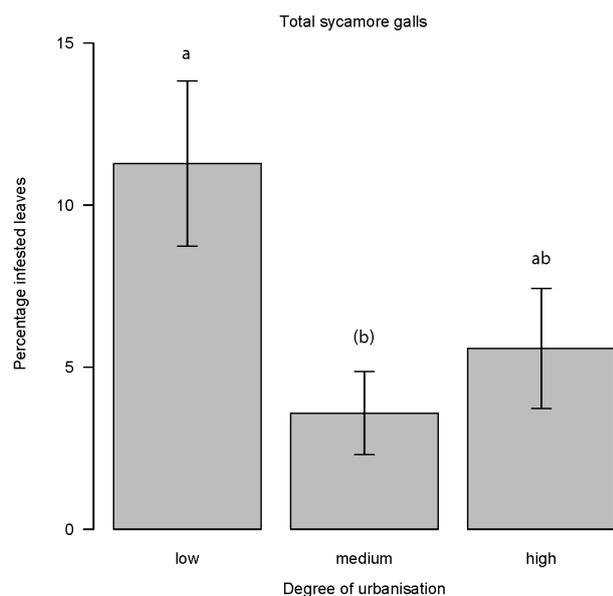
On the 328 sycamore trees, 595 out of 8,276 (7.2%) leaves were infested with galls. On the 315 beech trees, 2,374 of 29,430 (8.1%) leaves were infested with galls. For 161 ash trees, 179 of 3,878 (4.6%) leaves were infested with galls.

### Effects of urbanisation and forest size on plant galls

Degree of urbanisation affected the percentage of sycamore leaves infested by galls (Fig. 1; Table S3a). The highest gall infestation rate was recorded in forests in areas with low compared to medium and high degrees of urbanisation (Fig. 1). Similarly, the degree of urbanisation affected the percentage of beech leaves infested with *M. fagi*, but not the percentage of beech leaves infested by total galls (Fig. 2; Table S3b). For ash leaves, gall infestation rate was not influenced by the degree of urbanisation.

Forest size did not affect the percentage of sycamore leaves infested by galls (Table S3a). Considering beech, increasing forest size did not affect the percentage of leaves infested by total galls, but percentage of leaves infested with *M. fagi* tended to be affected by forest size (Fig. 3; Table S3b). For ash, the percentage of leaves infested by galls was not influenced by forest size (Table S3c). The degree of urbanisation and forest size interaction was not significant for any of the tree species (Table S3a–c).

The assessed forest site characteristics influenced gall infestation rate of the three tree species to a different degree. For sycamore, *P. aceris* infestation rate was significantly



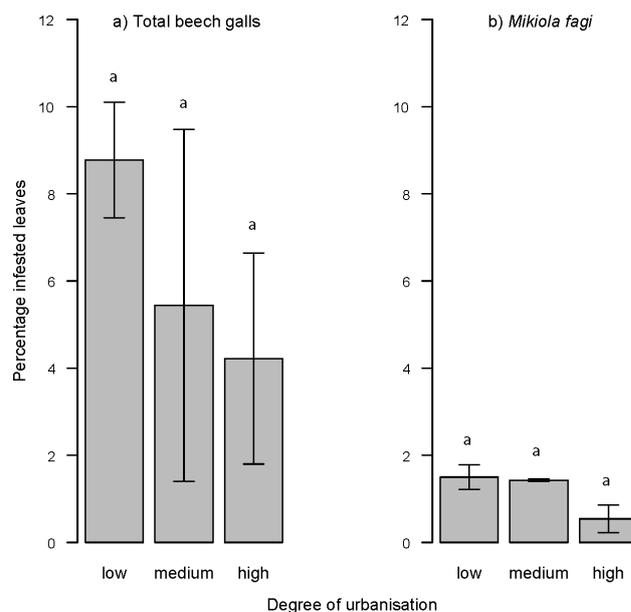
**Fig. 1.** The percentage of sycamore (*Acer pseudoplatanus*) leaves infested with galls in areas with different degrees of urbanisation. Different letters indicate significant differences among different degrees of urbanisation (low, medium, high), Tukey HSD,  $P < 0.05$ . Mean values  $\pm$  SE are presented ( $n = 19$ ).

influenced by the total number of leaves and canopy closure (Table S3a). For beech, *M. fagi* infestation rate significantly increased with increasing plant height ( $r_s = 0.71$ ,  $n = 12$ ,  $P = 0.010$ ; Table S3b). For ash, *Psyllopsis* sp. infestation rate tended to increase with increasing shrub species richness ( $r_s = 0.45$ ,  $n = 19$ ,  $P = 0.053$ ; Table S3c).

In addition, a subset of leaves was sampled to assess the percentage mortality of the gallers. Out of a total of 863 individual galls recorded on the 346 infested leaves sampled in the 20 forest sites, 494 of galls were those of gall midges (43 *D. fraxini*, 300 *H. annulipes*, 151 *M. fagi*) and 369 were those of gall wasps (*P. aceris*). The total percentage mortality of the sycamore gall wasp *P. aceris* was high (mean: 89.8%; Table S4). The percentage mortality of the two gall midges, *M. fagi* and *H. annulipes*, recorded on beech leaves was 47.0% and 80.3%, respectively (Table S4). For the ash gall midge *D. fraxini*, none of the galls collected in six forest sites were parasitized or killed by predators or fungus. However, for more than one third the galls fate was unknown (37.4%; 0–100%). Due to the uneven distribution of leaves with galls sampled in the forest, mortality could not be analysed statistically.

### Effects of urbanisation and forest size on leaf damage

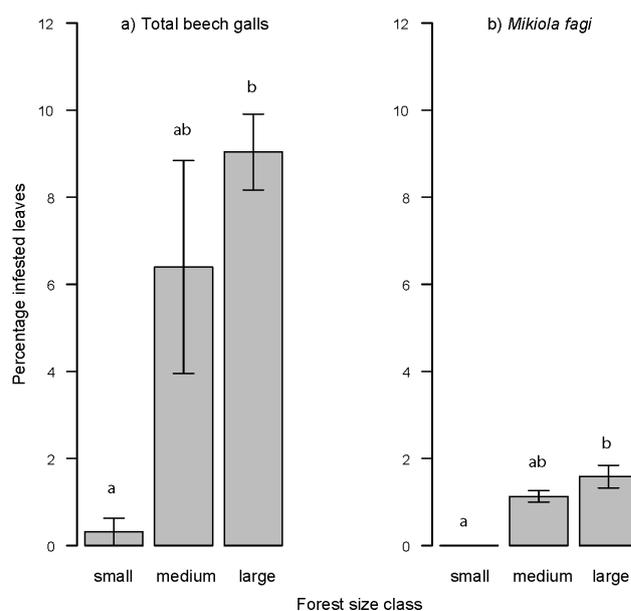
Overall 84% of the leaves collected were damaged (877 from a total of 1,044 leaves). Considering tree species, 86.2% of sycamore leaves (357 from 414), 80.5% of beech leaves (256 from 318) and 84.6% of ash leaves (264 from 312) were damaged. The percentage of leaf area damaged averaged 3.8% for all three species combined (3.7% for sycamore, 3.3% beech and 4.3% ash). Damage by chewing insects was the most common type (54.7% leaves damaged; 4.4% leaf area damaged); followed by mining



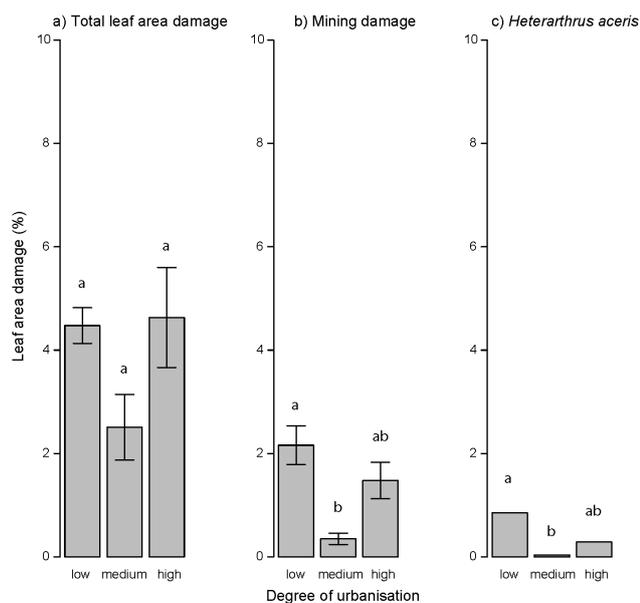
**Fig. 2.** The percentage of beech tree (*Fagus sylvatica*) leaves infested with total galls (a) and those of the gall midge *Mikiola fagi* (b) in areas with different degrees of urbanisation. Different letters indicate significant differences among different degrees of urbanisation (low, medium, high), Tukey HSD,  $P < 0.05$ . Mean values  $\pm$  SE are presented ( $n = 12$ ).

(26.2%; 5.0%); and lastly by fungi (3.2%; 2.8%). Mean leaf area damaged was not correlated with gall infestation rate in any of the three tree species (in all cases  $P > 0.23$ ; Fig. S1a–c).

Damage by nine herbivore and two fungal species were recorded on sycamore leaves (Table S5). The most common damage on sycamore leaves were caused by the saw-



**Fig. 3.** The percentage of beech tree (*Fagus sylvatica*) leaves infested with total galls (a) and those of the gall midge *Mikiola fagi* (b) in different sized forests. Different letters indicate significant differences among different forest sizes (small, medium, large), Tukey HSD,  $P < 0.05$ . Mean values  $\pm$  SE are presented ( $n = 12$ ).

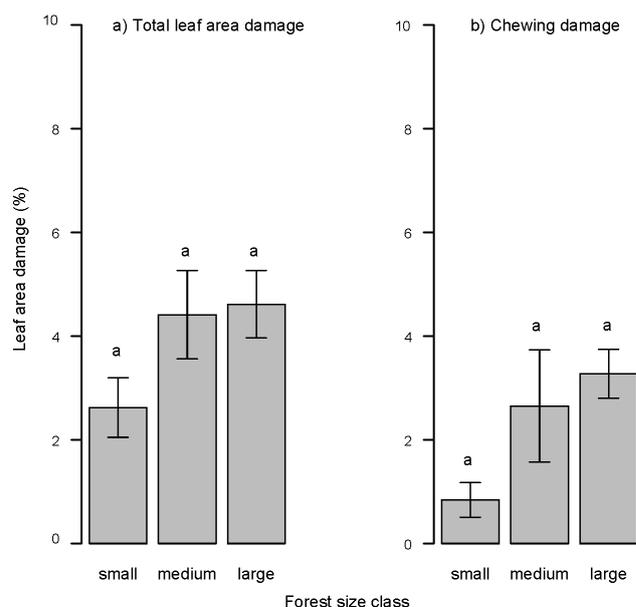


**Fig. 4.** The percentage of total leaf area damaged on sycamore (*Acer pseudoplatanus*) (a), the percentage of leaf area damaged by mining arthropods (b) and the percentage leaf area damaged by the sawfly *Heterarthrus aceris* (c) in areas with different degrees of urbanisation. Different letters indicate significant differences among different degrees of urbanisation (low, medium, high), Tukey HSD,  $P < 0.05$ . Mean values  $\pm$  SE are presented ( $n = 19$ ).

fly *Heterarthrus cuneifrons* (10.4%; 0.49%; percentage of leaves damaged and mean percentage of leaf area damaged), the moth *Stigmella speciosa* (10.1%; 0.31%), the sawfly *Heterarthrus aceris* (8.7%; 0.43%) and the fungus *Rhytisma acerinum* (7.5%; 0.17%). Damage of six herbivorous species was recorded on beech leaves. The most common damage was caused by the weevil *Orchestes fagi* (chewing damage: 28.9%; 0.97%, and mining damage: 7.2%; 0.22%) and the moth *Phyllonorycter maestingella* (5.7%; 0.31%). On ash leaves, three species of herbivorous moths were recorded, namely *Gracillaria syringella* (8.3%; 1.29%), *Prays fraxinella* (4.2%; 0.13%) and *Coleophora badiipennella* (1.3%; 0.02%; Table S5).

Degree of urbanisation affected the total percentage of leaf area damaged in sycamore (Fig. 4; Table S6a). Among the three damage types, urbanisation affected the percentage of leaf area damaged by mining insects. Furthermore, the percentage of leaf area damaged by the sawfly *Heterarthrus aceris* was influenced by the degree of urbanisation (Fig. 4; Table S6a). For beech and ash, the degree of urbanisation did not influence the percentage of leaf area damaged (Table S6b, c).

Increasing forest size significantly increased the total percentage of leaf area damage on sycamore (Fig. 5; Table S6a). The same pattern was found for the percentage of sycamore leaf area damaged by chewing insects. For beech and ash leaves, forest size was affected by neither total percentage leaf area damaged nor damage types. The significant interaction between urbanisation and forest size was a result of a lower incidence of chewing damage in small forests than in large forests in highly urbanised areas (Table S6b).



**Fig. 5.** The percentage of total leaf area damaged on sycamore (*Acer pseudoplatanus*) (a) and the percentage of leaf area damaged by chewing arthropods (b) in different sized forests. Different letters indicate significant differences among different forest sizes (small, medium, large), Tukey HSD,  $P < 0.05$ . Mean values  $\pm$  SE are presented ( $n = 19$ ).

Environmental characteristics of forest sites influenced leaf area damage in various ways. Considering sycamore, chewing leaf area damage was influenced by total number of leaves and increased with increasing canopy closure ( $r_s = 0.48$ ,  $n = 19$ ,  $P = 0.041$ ; Table S6a). For beech, mining damage was affected by tree richness and positively correlated with tree density ( $r_s = 0.75$ ,  $n = 12$ ,  $P = 0.005$ ; Table S6b). Regarding ash, total leaf area damage was influenced by tree richness and increased with increasing soil moisture ( $r_s = 0.62$ ,  $n = 19$ ,  $P = 0.006$ ; Table S6c). Furthermore, chewing leaf area damage of ash was influenced by total number of leaves and was positively correlated with soil moisture ( $r_s = 0.48$ ,  $n = 19$ ,  $P = 0.041$ ). Ash mining leaf area damage and damage by *G. syringella* was influenced by tree richness (Table S6c).

## DISCUSSION

### Effects of urbanisation and forest size on plant galls

Our study showed both tree species-specific and arthropod species-specific responses of gall infestation to the degree of urbanisation and forest size. For beech trees, the gall infestation rate at the leaf level (7.0%) reported here is similar to that reported in a German beech forest (10%; Gossner et al., 2014), but lower than in a beech forest in Poland (35%; Pilichowski & Giertych, 2018). Gall infestation rate was, however, slightly higher than the average of 4.4% recorded in temperate forests (Kozlov et al., 2015).

In this study, an increase in the degree of urbanisation had a negative effect on gall infestation rates, especially for the beech gall midge *M. fagi*. Although some galling species may be found to be more prevalent in urban areas

(Frankie et al., 1987), our result is consistent with findings of McGeoch & Chown (1997) and Mingaleva et al. (2011), who report an overall reduction in gall infestation rate on seven tree species in urban areas (but these studies did not investigate beech, *Fagus sylvatica*) and Segebade & Schaefer (1979), who found *M. fagi* to be completely absent in urban trees. In sycamore trees, our result that leaf gall infestation was highest in low urbanised areas, contrasts previous findings of Skrzypczyńska (2004) and Segebade & Schaefer (1979), who reported higher infestation rates of *Aceria cephalonea* and *Aceria macrorhyncha* in urban areas.

Various factors may contribute to the distribution patterns of galls, including forest fragmentation, abiotic factors such as the thermal radiation from urban environments and humidity, spatial distribution of trees, leaf quality, availability of overwintering sites and dispersal capabilities.

Several studies reported higher gall infestation rates in small forest fragments than in large forests due to edge effects resulting in increased stress of the plants (Araújo & Espírito-Santo Filho, 2012) or increased plant vigour, reduced mortality or changes in microclimate (Akkuzu et al., 2015; Maldonado-López et al., 2015; Kelch et al., 2016). However, none of these studies were conducted in forests embedded in an urban matrix. In our study, we recorded that the infestation rate of the beech gall midge *M. fagi* was more pronounced in large than in small forests.

Forests of various sizes may also differ in their local climatic conditions. In particular, small urban forests are more subject to higher temperatures and lower humidity (Marzluff et al., 2008; Dale & Frank, 2014), which can negatively (Valladares et al., 2006) or positively impact herbivorous insects (Youngsteadt et al., 2015). A previous study conducted in the same forest sites could not detect any temperature increase in forests in highly urbanised areas (Melliger et al., 2017), probably because forests can buffer part of the elevated temperature in urban areas (Long et al., 2019).

Galling species are able to manipulate their micro-environment, for example, by regulating the humidity inside the galls (Fernandes & Price, 1992). Galling insects have been found to be more species-rich in xero-thermic regions in the USA and Brazil (Price et al., 1987). A vertical stratification sampling of beech leaves in a rural German beech forest showed that *M. fagi* infestation was not affected by differences in temperature and humidity levels (Stiegel & Mantilla-Contreras, 2018). Although beech trees are sensitive to water deficit, *M. fagi* is probably not more vulnerable to the drier climatic conditions in small urban forests.

The gall midge *M. fagi* can exploit beech trees in a wide range of environments, which can result in potential outbreaks (Skuhrový & Skuhrová, 1996; Urban, 2000). A higher abundance of beech trees caused overall a positive effect on gall midge incidence (Mangels et al., 2015). Similarly, the larger forests in our study had on average higher densities of beech saplings and thus higher beech gall infestation rates. In accordance, *M. fagi* gall infestation rates

were positively related to tree height. These relationships can be explained by the resource concentration hypothesis (Root, 1973), which states a greater prevalence of host plants results in larger herbivore populations (Schnitzler et al., 2011).

Urban forests are frequently used for recreation, which can result in soil compaction and reduction in the amount of leaf litter (New, 2015). In the forests examined, a reduced litter biomass was recorded in small forests (Melliger et al., 2017). This may negatively impact the litter overwintering habitat for the pupae of *M. fagi*, as suggested by Segebade & Schaefer (1979).

Fragmentation decreases the connectivity between habitat patches by disrupting insect movement, which reduces the probability of colonizing more isolated habitat patches (Harvey & MacDougall, 2015). It is expected that some traits such as body size and high resource specialisation are the key factors, which result in a more pronounced negative response to spatial scale (Tscharntke & Brandl, 2004). Therefore, it is possible that small host-plant specialist gall midges (Carneiro et al., 2009), with relatively short active dispersal ranges from 1–7 m for *Rhopalomyia californica* to 500 m for *Sitodiplosis mosellana* (Briggs & Latto, 2000; Hao et al., 2013), could be negatively affected by increasing habitat fragmentation. A study on vertical zonation in North western Switzerland indicated that females of *M. fagi* were capable of flying up to the canopy (>30 m) for oviposition (Kampichler & Teschner, 2002), but greater flight distances have not been recorded for this species. This negative fragmentation effect may be even more pronounced during passive long-distance dispersal attempts in a complex (urban) landscape than in a homogenous landscape due to a lower probability of randomly reaching a suitable habitat patch (Miao et al., 2013; Martinson & Fagan, 2014; O'Rourke & Petersen 2017).

According to the predator-avoidance hypothesis, urbanisation can result in a reduced parasitism rate of plant-galling arthropods in urban areas (Frankie et al., 1987; McIntyre, 2000). However, we were not able to test this hypothesis. Nonetheless, the low parasitism rate recorded in the gall midges *M. fagi*, *H. annulipes* and *D. fraxini* could be a result of their hypersensitivity (localised resistance of host plant against pathogens), being the main cause for larval mortality early in development, which prevents the possibility of parasitism (Fernandes et al., 2003; Pili-chowski & Giertych, 2017). In contrast, high parasitism rates, reported here for the sycamore gall wasp *P. aceris* (71.4–100%) have also been reported in other gall wasps (Stone et al., 2002).

#### Effects of urbanisation and forest size on leaf damage

We recorded an overall high percentage (84%) of leaves damaged, but low mean leaf area damaged (3.8%) by herbivorous arthropods. Independent of different sample sizes, the extent of leaf area damages was very similar to that reported in other studies in beech forests (80% of leaves and 6% of leaf area damaged; Gossner et al., 2014) and in urban areas (87% of leaves and <5% of leaf area damaged;

Christie & Hochuli, 2005). However, higher leaf area damages were reported in temperate regions (7.1%; Coley & Barone, 1996; and 7.6%; Kozlov et al., 2015).

We found host-specific responses to urbanisation, which were only significant in sycamore. The highest level of sycamore leaf damage was found in highly urbanised sites, supporting the results of other studies (e.g. Christie & Hochuli, 2005; Raupp et al., 2010; Meineke et al., 2013). Considering exclusively sycamore and beech leaf mining damage, its extent was most pronounced in forests situated in areas with a low degree of urbanisation. This reflects findings of prior studies that showed reduced leaf damage in urban trees (Nuckols & Connor, 1995; Mingaleva et al., 2011; Kozlov et al., 2017). This pattern was explained by predatory activity of generalists including ants and birds in urban areas (Kozlov et al., 2017). However, a study on oak herbivory found no effects of urbanisation on leaf damage by mining arthropods, but rather a 30% reduction in chewing damage in urban areas (Moreira et al., 2019). Although we could not find an overall negative effect of urbanisation on chewing damage on sycamore, the interaction with forest size revealed a combined negative effect causing a lower sycamore chewing damage level in small forests, especially in highly urbanised areas.

In our study, small forests had the lowest total leaf damage and chewing damage in sycamore. Reduced chewing damage in small forests compared to large continuous forests was also reported by Ruiz-Guerra et al. (2010). The observed reduction in leaf damage could be a result of a negative effect of fragmentation on the abundance of folivorous arthropods (Valladares et al., 2006; Martinson & Fagan, 2014; Chávez-Pesqueira et al., 2015). Environmental variables have the potential to influence the abundance of particular leaf mining species (Raupp et al., 2010; Stiegel & Mantilla-Contreras, 2018; Vidal & Murphy, 2018). Our result that both the total leaf area damage on ash and chewing damage on ash were positively affected by soil moisture, contrasts previous findings of a negative relationship between urban heat stress and the extent of insect pest infestations (Meineke & Frank, 2018).

In conclusion, our study revealed that urbanisation and forest size have the potential to disrupt plant-arthropod interactions. The varying responses of galling and other herbivorous arthropods to urbanisation and forest size may be a result of local environmental conditions, tree-specific responses as well as herbivore species-specific responses (e.g. limited dispersal capabilities, host specificity). Nevertheless, we were able to show that the effects of urbanisation and a reduction of forest size did not benefit most plant galling or herbivorous arthropods, but rather negatively impacted the infestation rates of some arthropods such as the beech galling midge, *M. fagi*.

**ACKNOWLEDGEMENTS.** We would like to thank the forest owners and foresters for allowing us access to the forests. We thank R. Askew and M. Skuhrová for advice with and help in species identification. Lastly, we would like to thank B. Braschler, T. Fayle and three anonymous reviewers for useful comments on the manuscript.

**AUTHOR CONTRIBUTIONS.** S. Meyer: field work, identification of arthropods, data analysis, manuscript writing; H.-P. Rusterholz: study design, data analysis, reviewed and edited the manuscript; B. Baur: study design, reviewed and edited the manuscript.

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Received April 15, 2019; revised and accepted December 27, 2019

Published online January 29, 2020

**Table S1.** Characteristics of the 20 deciduous forest sites examined. Percentage sealed area within a radius of 500 m was assigned to three degrees of urbanisation: low (<15%), medium (15–30%) or high (>30%). The forests were categorised into three forest size classes: small (<4,000 m<sup>2</sup>), medium-sized (4,000–10,000 m<sup>2</sup>), or large (>10,000 m<sup>2</sup>). GPS coordinates and elevation were obtained from www.map.geo.admin.ch.

Forest	GPS coordinates (m. a.s.l.)	Elevation (m. a.s.l.)	Sealed area within a radius of 500 m (%)	Urbanisation level	Forest area (m <sup>2</sup> )	Forest size class	Type of forest	Forest age (years)	Soil organic matter	Soil moisture	Canopy closure (%)	Shrub richness (median)	Tree richness (median)
Bärlauchweglein	47°34'08"N 7°39'06"E	346	12	low	8908	medium-sized	planted	58	22.3	26.91	94.2	5	2
Breite	47°33'10"N 7°36'51"E	264	39	high	7049	medium-sized	planted	58	25.58	17.71	96	6.5	3.5
Chrischona	47°34'30"N 7°40'35"E	485	4	low	14000	large	forest	>200	23.55	32.58	93.05	4	3
Friedhof Riehen T	47°33'56"N 7°38'29"E	276	25	medium	4234	medium-sized	planted	81	10.58	14.25	92.88	6	1.5
Friedhof Riehen Wald	47°33'49"N 7°38'42"E	304	12	low	4034	medium-sized	forest	>200	13.12	21.3	95.5	6.5	1
Fürstensteinerstrasse	47°32'11"N 7°36'07"E	299	54	high	3244	small	fragment	134	21.67	25.13	96.9	6	3
Glögglihof	47°34'52"N 7°38'53"E	280	33	high	5765	medium-sized	planted	131	16.76	22.06	98.3	5	3
Gundeldingerrain	47°32'17"N 7°35'39"E	301	44	high	2285	small	planted	74	16.3	23.91	95.86	5.5	3.5
Hohlweg	47°35'15"N 7°39'57"E	332	10	low	2800	small	planted	58	19.05	18.75	97.44	9	3.5
Jakobsbergerholz	47°31'57"N 7°36'10"E	305	44	high	14000	large	fragment	134	13.54	15.57	98.21	5.5	2.5
Jakobsbergerhölzli	47°31'49"N 7°35'50"E	336	22	medium	21000	large	fragment	134	13.76	17.93	97.64	5.5	2
Lange Erlen	47°34'33"N 7°36'18"E	252	20	medium	21000	large	forest	>200	12.57	19.11	97.86	4.5	2.5
Linsberg	47°34'25"N 7°39'52"E	425	10	low	50000	large	forest	>200	20.83	25.26	96.91	9	6
Maienbühl	47°35'18"N 7°40'10"E	349	3	low	34000	large	forest	>200	20.18	23.77	97.14	2.5	1.5
Margarethenpark	47°32'31"N 7°35'01"E	301	35	high	19000	large	fragment	136	13.39	20.53	96.09	6	3
Mooswaldli	47°34'51"N 7°39'37"E	297	16	medium	4686	medium-sized	fragment	131	15.14	27.34	94.71	6	2.5
Salamanderwegli	47°35'05"N 7°40'09"E	317	8	low	4061	medium-sized	planted	95	13.57	23.2	97.28	2	2.5
Singerstrasse	47°32'49"N 7°36'50"E	276	70	high	1084	small	planted	113	28.09	14.86	98.1	2.5	2
Teich	47°35'12"N 7°38'52"E	275	17	medium	258	small	planted	58	18.15	13.86	93.9	3	3
Wenkenköpfl	47°34'29"N 7°39'29"E	372	12	low	36000	large	fragment	131	23.3	27.11	97.8	7	2

**Table S2.** Inter-correlations (Spearman correlations) among tree and forest site characteristics.

(a) Sycamore tree characteristics	
Number of leaves vs. average tree height	$r_s = -0.27$ , $n = 19$ , $P = 0.263$
<b>Number of leaves vs. density of trees</b>	<b><math>r_s = 0.89</math>, <math>n = 19</math>, <math>P &lt; 0.001</math></b>
<b>Average tree height vs. density of trees</b>	<b><math>r_s = -0.54</math>, <math>n = 19</math>, <math>P = 0.017</math></b>
Canopy closure vs. average tree height	$r_s = -0.03$ , $n = 19$ , $P = 0.918$
Canopy closure vs. density of trees	$r_s = 0.11$ , $n = 19$ , $P = 0.642$
(b) Beech tree characteristics	
Number of leaves vs. average tree height	$r_s = 0.48$ , $n = 12$ , $P = 0.115$
<b>Number of leaves vs. density of trees</b>	<b><math>r_s = 0.82</math>, <math>n = 12</math>, <math>P &lt; 0.001</math></b>
Average tree height vs. density of trees	$r_s = 0.01$ , $n = 12$ , $P = 0.974$
<b>Canopy closure vs. average tree height</b>	<b><math>r_s = 0.64</math>, <math>n = 12</math>, <math>P = 0.028</math></b>
Canopy closure vs. density of trees	$r_s = -0.53$ , $n = 12$ , $P = 0.079$
(c) Ash tree characteristics	
Number of leaves vs. average tree height	$r_s = 0.17$ , $n = 19$ , $P = 0.484$
<b>Number of leaves vs. density of trees</b>	<b><math>r_s = 0.71</math>, <math>n = 19</math>, <math>P &lt; 0.001</math></b>
Average tree height vs. density of trees	$r_s = -0.40$ , $n = 19$ , $P = 0.092$
Canopy closure vs. average tree height	$r_s = 0.16$ , $n = 19$ , $P = 0.498$
Canopy closure vs. density of trees	$r_s = -0.30$ , $n = 19$ , $P = 0.204$

(d) Sycamore forest characteristics	
Soil moisture vs. soil organic matter content	$r_s = 0.26$ , $n = 19$ , $P = 0.275$
Soil moisture vs. canopy closure	$r_s = 0.16$ , $n = 19$ , $P = 0.522$
Canopy closure vs. soil organic matter content	$r_s = -0.02$ , $n = 19$ , $P = 0.928$
Canopy closure vs. shrub richness	$r_s = -0.09$ , $n = 19$ , $P = 0.708$
Canopy closure vs. tree richness	$r_s = -0.30$ , $n = 19$ , $P = 0.916$
Tree richness vs. shrub richness	$r_s = 0.15$ , $n = 19$ , $P = 0.540$
(e) Beech forest characteristics	
Soil moisture vs. soil organic matter content	$r_s = 0.57$ , $n = 12$ , $P = 0.059$
Soil moisture vs. canopy closure	$r_s = 0.21$ , $n = 12$ , $P = 0.514$
Canopy closure vs. soil organic matter content	$r_s = -0.14$ , $n = 12$ , $P = 0.667$
Canopy closure vs. shrub richness	$r_s = 0.14$ , $n = 12$ , $P = 0.661$
Canopy closure vs. tree richness	$r_s = -0.16$ , $n = 12$ , $P = 0.618$
Tree richness vs. shrub richness	$r_s = 0.07$ , $n = 12$ , $P = 0.832$
(f) Ash forest characteristics	
Soil moisture vs. soil organic matter content	$r_s = 0.21$ , $n = 19$ , $P = 0.394$
Soil moisture vs. canopy closure	$r_s = 0.36$ , $n = 19$ , $P = 0.135$
Canopy closure vs. soil organic matter content	$r_s = 0.15$ , $n = 19$ , $P = 0.541$
Canopy closure vs. shrub richness	$r_s = 0.04$ , $n = 19$ , $P = 0.861$
Canopy closure vs. tree richness	$r_s = 0.19$ , $n = 19$ , $P = 0.443$
Tree richness vs. shrub richness	$r_s = 0.35$ , $n = 19$ , $P = 0.143$

(g) Herbivore damage (% leaf area loss) and % leaves infested with galls

Sycamore	Herbivore damage vs. gall infestation rate	$r_s = 0.02$ , $n = 19$ , $P = 0.926$
Beech	Herbivore damage vs. gall infestation rate	$r_s = 0.37$ , $n = 12$ , $P = 0.238$
Ash	Herbivore damage vs. gall infestation rate	$r_s = 0.17$ , $n = 19$ , $P = 0.446$

**Table S3.** Summary of ANCOVA analyses examining the effects of urbanisation, forest size, tree height, total number of leaves, and density of trees (number of tree individuals/4 m<sup>2</sup>), soil organic matter, soil moisture, canopy closure, shrub richness and tree richness, on the percentage of leaves infested by galls for (a) sycamore, (b) beech and (c) ash.

(a) Sycamore (*Acer pseudoplatanus*)

	Percentage of leaves infested by								
	Total galls			Gall mites <i>Aceria</i> spp.			Gall wasp <i>Pediaspis aceris</i>		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,3	11.85	<b>0.038</b>	2,8	1.21	0.347	2,10	1.87	0.204
Forest size	2,3	1.64	0.833	2,8	1.01	0.408	2,10	2.37	0.143
Tree height <sup>1</sup>	1,3	6.80	0.080	–	–	–	1,10	2.44	0.149
Total number of leaves	1,3	6.41	0.085	1,8	2.15	0.181	1,10	6.81	<b>0.026</b>
Soil organic matter	1,3	6.85	0.079	–	–	–	1,10	3.68	0.084
Soil moisture	1,3	3.98	0.140	–	–	–	–	–	–
Canopy closure	1,3	6.08	0.090	–	–	–	1,10	7.40	<b>0.022</b>
Shrub richness	1,3	6.04	0.091	–	–	–	–	–	–
Tree richness	1,3	3.74	0.149	1,8	1.04	0.338	–	–	–
Urbanisation*forest size class	4,3	2.45	0.244	4,8	1.00	0.461	–	–	–

<sup>1</sup> sqrt-transformed; “–” not included in the model due to the step-wise reduction procedure. Due to inter-correlation the following variable was not included in the model: Density of trees. Significant effects ( $P < 0.05$ ) are presented in bold.

(b) Beech (*Fagus sylvatica*)

	Percentage of leaves infested by								
	Total galls			Gall midge <i>Mikiola fagi</i>			Gall midge <i>Hartigiola annulipes</i>		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,6	2.42	0.169	2,6	7.30	<b>0.025</b>	2,7	1.44	0.300
Forest size	2,6	3.35	0.105	2,6	4.95	0.054	2,7	2.12	0.191
Tree height <sup>1</sup>	1,6	1.36	0.287	1,6	6.55	<b>0.043</b>	–	–	–
Density of trees <sup>2</sup>	–	–	–	–	–	–	–	–	–
Soil organic matter	–	–	–	–	–	–	–	–	–
Soil moisture	–	–	–	–	–	–	–	–	–
Tree richness	–	–	–	–	–	–	–	–	–

<sup>1</sup> sqrt-transformed; <sup>2</sup> log-transformed. Due to inter-correlations the following variables were not included in the model: Total number of leaves and canopy closure. Due to limited degrees of freedom the variable shrub richness and the interaction, urbanisation\*forest size class was not calculated. “–” not included in the model due to the step-wise reduction procedure. Significant effects ( $P < 0.05$ ) are presented in bold.

(c) Ash (*Fraxinus excelsior*)

	Percentage of leaves infested by					
	Total galls			Psyllid <i>Psyllopsis</i> sp.		
	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,10	1.71	0.230	2,10	2.36	0.145
Forest size	2,10	0.93	0.427	2,14	1.54	0.262
Tree height <sup>1</sup>	1,10	2.93	0.118	1,10	4.45	0.061
Density of trees <sup>2</sup>	1,10	1.81	0.208	1,10	2.27	0.163
Soil organic matter	1,10	1.27	0.286	1,10	1.55	0.241
Soil moisture	–	–	–	–	–	–
Canopy closure	–	–	–	–	–	–
Shrub richness	1,10	2.03	0.185	1,10	5.22	<b>0.046</b>
Tree richness	–	–	–	–	–	–
Urbanisation*forest size class	–	–	–	–	–	–

<sup>1</sup> sqrt-transformed; <sup>2</sup> log-transformed. Due to inter-correlation the following variable was not included in the model: Total number of leaves. “–” not included in the model due to the step-wise reduction procedure. Significant effects ( $P < 0.05$ ) are presented in bold.

**Table S4.** Total mortality of sycamore gall wasp *Pediaspis aceris* (a), and gall midges *Mikiola fagi* (b), *Hartigiola annulipes* (c) and *Dasineura fraxini* (d). Mean values and range in (%) are given for the different mortality factors: Parasitism, fungal attack, predation, unknown (empty galls), total mortality (sum of parasitism, fungi, predation, and unknown mortality causes), and none (original galler still present i.e. no mortality).

Mortality factor	Mean (%)	Range (%)
(a) Sycamore gall wasp <i>Pediaspis aceris</i>		
Parasitism	46.7	12.5–75.0
<i>Dichatomus acerinus</i>	24.3	0–56.3
<i>Aulogygnus aceris</i>	9.4	0–50
Indistinguishable parasitoid larvae	13.0	0–25.2
Fungi	5.7	0–50.0
Predation	1.1	0–6.9
Unknown	36.4	0–78.6
<b>Total mortality</b>	<b>89.8</b>	<b>71.4–100</b>
None	10.2	0–28.6

(b) Beech gall midge <i>Mikiola fagi</i>		
Parasitism	10.1	0–16.7
<i>Aprostecus</i> sp.	9.6	0–16.7
<i>Aprostecus elongatus</i>	0.5	0–4.5
Fungi	0	0
Predation	2.4	0–15.0
Unknown	34.5	0–71.4
Total mortality	47.0	0–85.7
None	53.0	14.3–100
(c) Beech gall midge <i>Hartigiola annulipes</i>		
Parasitism	2.4	0–20
<i>Aprostecus</i> sp.	2.4	0–20
<i>Aprostecus elongatus</i>	0	0
Fungi	0	0
Predation	0	0
Unknown	77.9	52.9–97.4
Total mortality	80.3	52.9–97.4
None	19.7	2.6–47.1
(d) Ash gall midge <i>Dasineura fraxini</i>		
Parasitism	0	0–0
Fungi	0	0
Predation	0	0
Unknown	37.4	0–100
Total mortality	37.4	0–100
None	62.6	0–100

**Table S5.** Arthropod and fungal species recorded on sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*), percentage of leaves damaged and frequency of occurrence of species-specific damage.

Plant species	Insect/fungal species	% leaves damaged	% leaf area damaged	Frequency of occurrence <sup>c</sup>	
Sycamore	<b><i>Heterarthrus cuneifrons</i></b> <sup>a</sup>	<b>10.39</b>	<b>0.49</b>	<b>12/19</b>	
	<b><i>Stigmella speciosa</i></b> <sup>a</sup>	<b>10.14</b>	<b>0.31</b>	<b>11/19</b>	
	<b><i>Heterarthrus aceris</i></b> <sup>a</sup>	<b>8.70</b>	<b>0.43</b>	<b>12/19</b>	
	<i>Heterarthrus leucomela</i> <sup>a</sup>	0.48	0.03	2/19	
	<i>Phyllonorycter geniculella</i> <sup>a</sup>	1.21	0.02	4/19	
	<i>Phyllonorycter platanoidella</i> <sup>a</sup>	0.48	0.01	1/19	
	<i>Cameraria ohridella</i> <sup>a</sup>	0.97	0.03	3/19	
	<i>Caloptilia hemidactylella</i> <sup>a</sup>	0.72	0.02	3/19	
	<i>Incurvaria pectinea</i> <sup>a</sup>	0.97	0.05	3/19	
	<i>Rhytisma acerinum</i> <sup>b</sup>	7.49	0.17	6/19	
	<i>Cristulariella depraedans</i> <sup>b</sup>	0.48	0.004	2/19	
	Beech	<b><i>Orchestes fagi</i></b> chewing <sup>a</sup>	<b>28.93</b>	<b>0.97</b>	<b>11/12</b>
		<i>Orchestes fagi</i> mining <sup>a</sup>	7.23	0.22	9/12
<i>Phyllonorycter maestingella</i> <sup>a</sup>		5.66	0.31	6/12	
<i>Incurvaria koernerella</i> <sup>a</sup>		0.31	<0.01	1/12	
<i>Incurvaria mascullella</i> <sup>a</sup>		0.63	0.01	2/12	
<i>Bucculatrix thoracella</i> <sup>a</sup>		0.31	<0.01	1/12	
<i>Stigmella hemargyrella</i> <sup>a</sup>		0.31	<0.01	1/12	
Ash		<b><i>Gracillaria syringella</i></b> <sup>a</sup>	<b>8.33</b>	<b>1.29</b>	<b>13/19</b>
	<i>Prays fraxinella</i> <sup>a</sup>	4.17	0.13	8/19	
	<i>Coleophora badiipennella</i> <sup>a</sup>	1.28	0.02	4/19	

<sup>a</sup> arthropod; <sup>b</sup> fungus; <sup>c</sup> frequency of occurrence of species-specific damage was derived from the number of forest sites a particular species of herbivore was present, related to the number of forest sites at which the host plant was present. Abundance of species in bold were statistically analysed. The remaining species were too rare for statistical analysis.

**Table S6.** Summary of ANCOVA analyses examining the effects of urbanisation, forest size, tree height, total number of leaves, density of trees (number of tree individuals/4 m<sup>2</sup>), soil organic matter, soil moisture, canopy closure, shrub richness and tree richness, on the percentage of leaf area damage by herbivorous arthropods and fungi for (a) sycamore, (b) beech and (c) ash.

(a) Sycamore (*Acer pseudoplatanus*)

	Total % damage			% chewing			% mining			Sawfly <i>Heterarthrus aceris</i>			Sawfly <i>Heterarthrus cuneifrons</i>			Moth <i>Stigmella speciosa</i>		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,11	3.98	<b>0.050</b>	2,3	5.60	0.097	2,7	6.81	<b>0.023</b>	2,8	11.79	<b>0.004</b>	2,13	1.22	0.328	2,9	2.52	0.135
Forest size	2,11	4.63	<b>0.035</b>	2,3	77.33	<b>0.002</b>	2,7	0.01	0.993	2,8	0.99	0.444	2,13	0.97	0.405	2,9	3.63	0.070
Tree height <sup>1</sup>	1,11	1.16	0.304	1,3	9.29	0.056	–	–	–	–	–	–	–	–	–	1,9	1.91	0.200
Total number of leaves	1,11	1.32	0.275	1,3	11.16	<b>0.044</b>	1,7	2.17	0.184	–	–	–	–	–	–	1,9	3.96	0.078
Soil organic matter	–	–	–	1,3	3.75	0.148	–	–	–	1,8	1.33	0.282	–	–	–	1,19	2.46	0.151
Soil moisture	–	–	–	1,3	5.88	0.094	–	–	–	–	–	–	–	–	–	1,9	1.80	0.213
Canopy closure	1,11	4.15	0.066	1,3	71.79	<b>0.003</b>	1,7	1.99	0.201	1,8	2.43	0.158	1,13	1.56	0.233	–	–	–
Shrub richness	–	–	–	1,3	2.72	0.198	1,7	2.24	0.178	–	–	–	–	–	–	–	–	–
Tree richness	–	–	–	1,3	7.00	0.077	–	–	–	–	–	–	–	–	–	1,9	1.97	0.194
Urbanisation*forest size class	–	–	–	4,3	14.19	<b>0.027</b>	4,7	1.21	0.386	4,8	1.55	0.276	–	–	–	–	–	–

<sup>1</sup> sqrt-transformed. Due to inter-correlation the following variable was not included in the model: Density of trees. Not included in the model due to the step-wise reduction procedure. Significant effects ( $P < 0.05$ ) are presented in bold.

(b) Beech (*Fagus sylvatica*)

	Total % damage			% chewing			% mining			Weevil <i>Orchestes fagi</i> chewing		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,4	3.27	0.144	2,4	1.06	0.428	2,2	16.95	0.056	2,5	3.98	0.093
Forest size	2,4	0.74	0.532	2,4	0.07	0.937	2,2	9.29	0.097	2,5	3.06	0.136
Tree height <sup>1</sup>	1,4	2.36	0.199	–	–	–	1,2	11.50	0.077	1,5	1.75	0.243
Density of trees <sup>2</sup>	–	–	–	1,4	2.06	0.224	1,2	32.09	<b>0.030</b>	–	–	–
Soil organic matter	1,4	1.28	0.321	1,4	1.05	0.364	1,2	1.77	0.315	–	–	–
Soil moisture	–	–	–	–	–	–	1,2	2.97	0.227	1,5	1.71	0.248
Tree richness	1,4	2.7	0.177	1,4	1.86	0.244	1,2	52.35	<b>0.019</b>	–	–	–

<sup>1</sup> sqrt-transformed; <sup>2</sup> log-transformed. Due to inter-correlations the following variables were not included in the model: Total number of leaves and canopy closure. Due to limited degrees of freedom the variable shrub richness and the interaction, urbanisation\*forest size class was not calculated. “–” not included in the model due to the step-wise reduction procedure. Significant effects ( $P < 0.05$ ) are presented in bold.

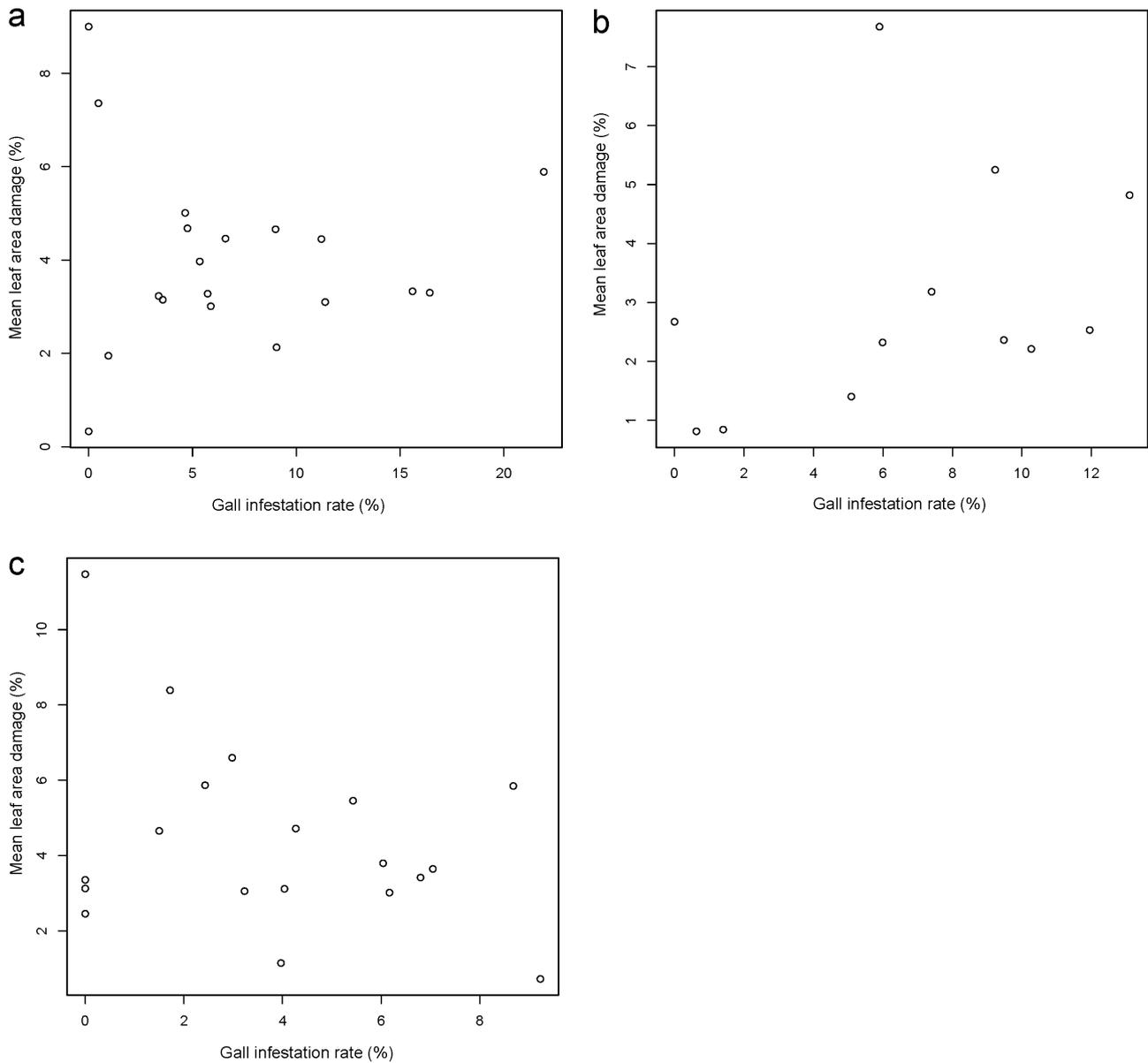
(c) Ash (*Fraxinus excelsior*)

	Total % damage			% chewing			% mining			Moth <i>Gracillaria syringella</i>		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Degree of urbanisation	2,10	3.41	0.074	2,9	0.40	0.683	2,9	2.84	0.111	2,7	2.02	0.203
Forest size	2,10	0.59	0.574	2,9	0.30	0.748	2,9	0.62	0.562	2,7	1.21	0.355
Tree height <sup>1</sup>	–	–	–	–	–	–	1,9	1.28	0.287	–	–	–
Total number of leaves	1,10	2.18	0.171	1,9	7.15	<b>0.026</b>	–	–	–	–	–	–
Soil organic matter	–	–	–	–	–	–	1,9	2.46	0.152	2,7	2.05	0.195
Soil moisture	1,10	8.25	<b>0.017</b>	1,9	7.95	<b>0.020</b>	1,9	1.08	0.325	–	–	–
Canopy closure	1,10	1.97	0.191	1,9	1.22	0.297	–	–	–	–	–	–
Shrub richness	–	–	–	1,9	1.94	0.197	1,9	2.14	0.178	1,7	1.02	0.347
Tree richness	1,10	5.52	<b>0.041</b>	1,9	1.12	0.318	1,9	14.51	<b>0.004</b>	1,7	11.92	<b>0.012</b>
Urbanisation* forest size class	–	–	–	–	–	–	–	–	–	4,7	1.25	0.372

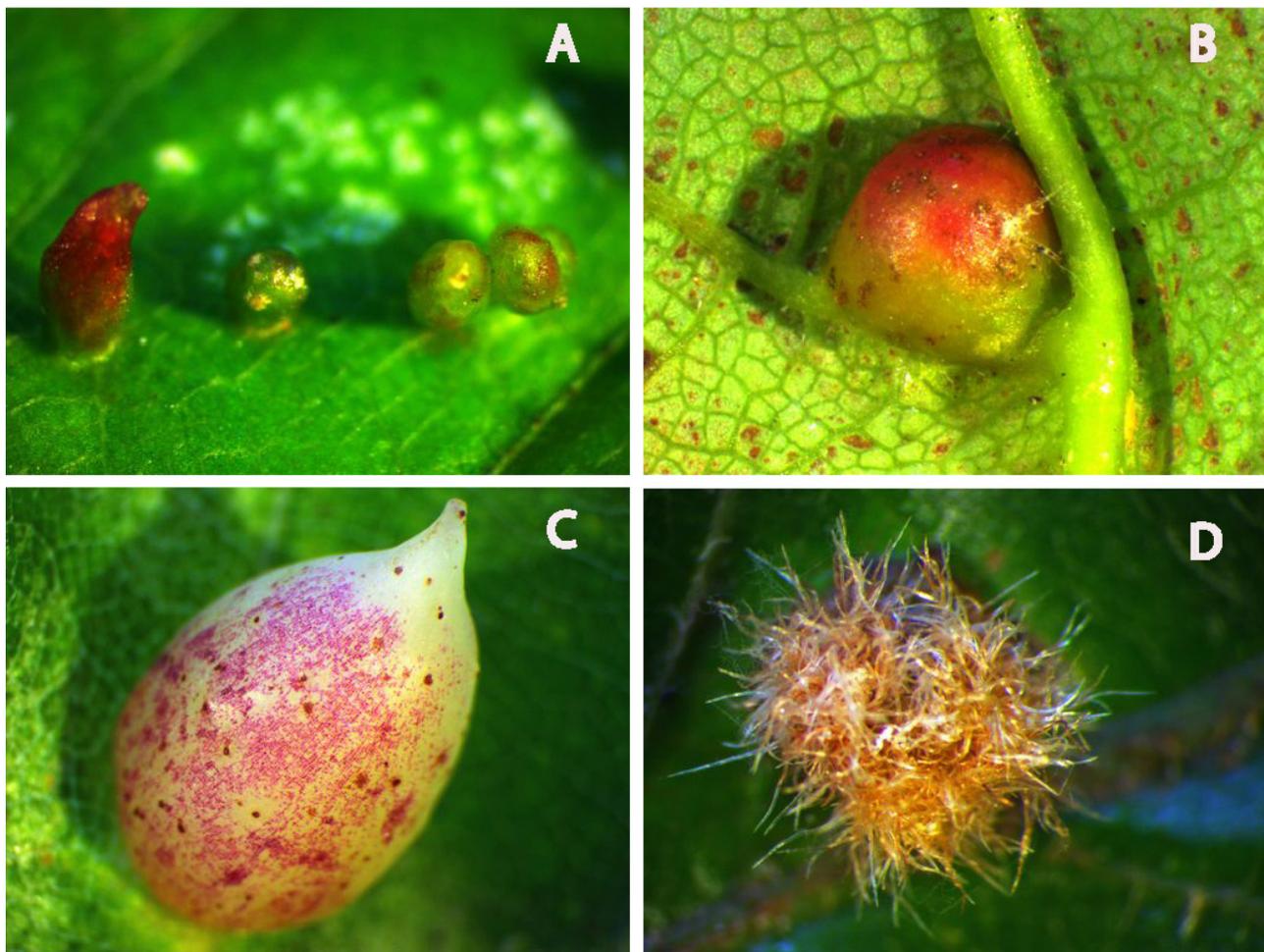
<sup>1</sup> sqrt-transformed. Due to inter-correlation the following variable was not included in the model: Density of trees. “–” not included in the model due to the step-wise reduction procedure. Significant effects ( $P < 0.05$ ) are presented in bold.

**Table S7.** Density of and percentage of the three focal tree species (sycamore, beech, and ash) in forests situated in areas with different degree of urbanisation and in forests of different sizes. Mean values ± SE are listed, n indicates the forest sample size.

	Density of sycamore saplings Mean ± SE	Density of beech saplings Mean ± SE	Density of ash saplings Mean ± SE	Sycamore saplings (%) Mean ± SE	Beech saplings (%) Mean ± SE	Ash saplings (%) Mean ± SE
Degree of urbanisation						
Low	19.1 ± 10.2 (n = 7)	18.6 ± 5.9 (n = 5)	6.4 ± 2.4 (n = 7)	42.4 ± 11.5	40.3 ± 14.5	17.2 ± 5.7
Medium	11.2 ± 5.6 (n = 5)	16.0 ± 9.4 (n = 3)	6.0 ± 2.0 (n = 5)	38.1 ± 14.3	32.7 ± 17.2	29.2 ± 13.6
High	23.6 ± 8.6 (n = 7)	13.0 ± 7.3 (n = 4)	11.6 ± 2.7 (n = 7)	49.3 ± 14.9	24.1 ± 12.2	26.6 ± 6.7
Forest size class						
Small	12.2 ± 5.6 (n = 5)	2.4 ± 2.2 (n = 2)	10.4 ± 2.4 (n = 5)	42.2 ± 11.9	7.4 ± 6.8	50.4 ± 9.4
Medium-sized	28.1 ± 11.6 (n = 7)	12.1 ± 6.8 (n = 4)	7.3 ± 2.7 (n = 6)	59.8 ± 11.8	23.2 ± 11.5	17.0 ± 7.0
Large	13.5 ± 5.2 (n = 7)	27.5 ± 6.5 (n = 6)	7.4 ± 2.5 (n = 8)	30.1 ± 13.0	56.0 ± 13.4	13.9 ± 3.9



**Fig. S1.** Scatterplots of the relationship between % leaf area damaged by herbivorous arthropods and gall infestation rates on leaves of (a) sycamore (Spearman rank correlation:  $r_s = 0.02$ ,  $n = 19$ ,  $P = 0.926$ ), (b) beech (Spearman rank correlation:  $r_s = 0.37$ ,  $n = 12$ ,  $P = 0.238$ ) and (c) ash (Spearman rank correlation:  $r_s = -0.19$ ,  $n = 19$ ,  $P = 0.446$ ).



**Fig. S2.** Plant-galling arthropods investigated in our study. A – sycamore gall mites (*Aceria* spp.); B – sycamore gall wasp (*Pediaspis aceris*); C – beech gall midges *Mikiola fagi*; D – *Hartigiola annulipes*.

## Chapter II

### **Leaf litter decomposition and litter fauna in urban forests: Effect of the degree of urbanisation and forest size**

Sandro Meyer, Hans-Peter Rusterholz, Jörg-Alfred Salamon, Bruno Baur

*Pedobiologia – Journal of Soil Ecology*, 2020, 78: 150609



## Leaf litter decomposition and litter fauna in urban forests: Effect of the degree of urbanisation and forest size



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### ARTICLE INFO

#### Keywords:

Acari  
Oribatid mites  
Collembola  
Species composition  
Traits  
Urban ecology

### ABSTRACT

Urbanisation is an important driver of environmental change and has the potential to alter the functioning of ecosystem processes. In urban forests, a key ecosystem process is litter decomposition, which is driven by the litter quality and composition of litter fauna. We examined whether the degree of urbanisation and forest size influence litter decomposition rates by the mesofauna in Basel (Switzerland). In order to assess the impact of the litter mesofauna on decomposition rates, we exposed litterbags with three mesh sizes (100 µm, 2 mm, and 4 mm) filled with a mixture of *Acer pseudoplatanus*, *Fagus sylvatica*, and *Fraxinus excelsior* litter for a period of 9 months in 17 forests of different size located in areas with different degrees of urbanisation. We recovered the litterbags after 3, 6, and 9 months, extracted the fauna and assessed the decomposition rates. We found that litter decomposition rates were negatively affected by the degree of urbanisation after 6 months, but not impacted by forest size. In terms of litter fauna, oribatid mites and Collembola were differently affected by urbanisation. Oribatid mites were most frequent in forests in moderately urbanised areas, whereas Collembola were more abundant in forests in highly urbanised areas. Abundances of Acari and Oribatida were lowest in medium-sized forests, while the abundance of Collembola was highest in large forests. Collembola species composition did not shift with urbanisation. Considering Collembola traits, species with globular bodies were most abundant in forests of medium-size and situated in low urbanised areas, whereas species with an eudaphic life form tended to be less abundant in small forests. We showed that urbanisation and forest size have the potential to impact litter fauna abundance and species with certain morphological and life form traits, which may alter the important ecosystem service of litter decomposition.

### 1. Introduction

The expansion of cities is an important driver of environmental change (Grimm et al., 2008; Kowarik, 2011). Reduced habitat size and increased spatial isolation are a result of urban sprawl and may change the dynamics of plant and animal populations (Niemelä, 1999). Furthermore, environmental conditions in urban habitats are affected by air pollution and changes in climatic conditions (urban heat island effect), allowing a longer growing season for plants and their associated invertebrate species (McIntyre et al., 2001).

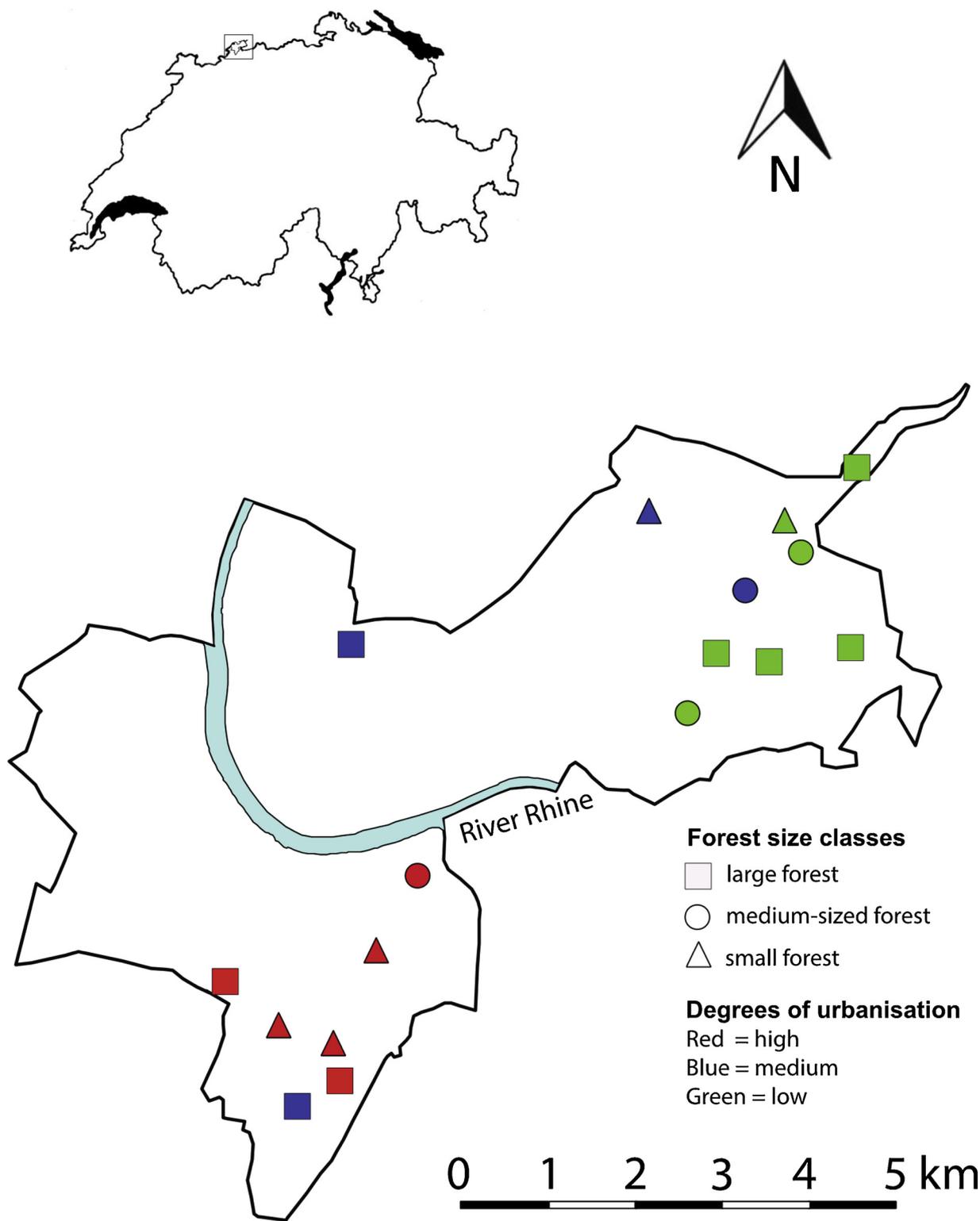
Forests are one of the most frequent semi-natural habitats in urban areas (Cvejić et al., 2015). These urban forests provide important ecosystem services such as water storage, climate regulation, improving air quality, carbon and nitrogen sequestration (Bolund and Hunhammar, 1999) and litter decomposition (Berg and McClaugherty, 2003). Litter decomposition facilitates the vital pathway of nutrient recycling and

soil formation in forests (Berg and McClaugherty, 2003; Jacob et al., 2010). Several factors can influence the decomposition rate of leaf litter such as the physicochemical litter traits (leaf toughness, nitrogen and lignin concentrations), regional climate (e.g. temperature, precipitation), local soil properties (e.g. soil moisture, pH and soil nutrient concentrations) and the composition and activity of decomposers (Hättenschwiler and Gasser, 2005; McClaugherty and Berg, 2011; García-Palacios et al., 2013). Urbanisation can increase soil temperature and reduce soil moisture and thus may influence the decomposition rate of leaf litter and alter its associated invertebrate fauna (Pouyat et al., 1997; Pouyat and Carreiro, 2003; Pavao-Zuckerman and Coleman, 2005).

Invertebrates associated with leaf litter can serve as model organisms to assess changes in litter decomposition and thus ecosystem functioning (Amossé et al., 2016; Maisto et al., 2017). Organisms involved in litter decomposition can be categorised into three groups

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**Fig. 1.** Location of study area in Northwestern Switzerland and the distribution of forests examined in Basel-Stadt. Based on the percentage cover of sealed area within the surrounding radius of 500 m, the forests were assigned into three urbanisation classes: low (green), medium (blue), and high (red). The forests were also assigned to three size classes: small (triangle), medium-sized (circle), and large forests (squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

based on their size. The micro-biota (< 100 μm) including bacteria and fungi are key players in leaf litter decomposition, because of their ability to break down recalcitrant compounds such as lignin, hemicellulose and cellulose (Schneider et al., 2012). The meso-fauna (body size: 200 μm – 2 mm) consists of various groups of invertebrates such as

Acari and Collembola that fragment the leaf litter (Moore et al., 1988; Hopkin, 1997; Walter and Proctor, 2013). The macro-fauna (body size: > 2 mm), in particular earthworms, have an important function to incorporate the leaf litter in the soil (Bottinelli et al., 2015).

In the past decades, there is growing evidence that urbanisation can

**Table 1**  
 Characteristics of the forests examined. Degree of urbanisation was assessed based on the percentage cover of sealed area within the surrounding radius of 500 m. Degree of urbanisation was assigned to three classes: low (< 15 %), medium (15–30 %) or high (> 30 %). The forests were also assigned to three size classes: small (< 4000 m<sup>2</sup>), medium-sized (> 4000–10,000 m<sup>2</sup>), or large (> 10,000 m<sup>2</sup>).

Forest	Coordinates	Elevation (m.a.s.l.)	Sealed area (%)	Degree of urbanisation	Forest area (m <sup>2</sup> )	Forest size class	Type of forest	Forest age (years)	Soil moisture content (%)	Soil organic matter content (%)	Canopy closure (%)
Bärlauchweglein	47°34'08"N 7°39'06"E	346	12	low	8908	medium-sized	planted	58	26.9	22.30	94.2
Breite	47°33'10"N 7°36'51"E	264	39	high	7049	medium-sized	fragment	58	17.7	25.58	96.0
Chrischona	47°34'30"N 7°40'35"E	485	4	low	14000	large	forest	NA	32.6	23.55	93.1
Fürstensteinstrasse	47°32'11"N 7°36'07"E	299	54	high	3244	small	fragment	134	25.1	21.67	96.9
Gundelinggerrain	47°32'17"N 7°35'39"E	301	44	high	2285	small	planted	74	23.9	16.30	95.9
Hohlweg	47°35'15"N 7°39'57"E	332	10	low	2800	small	planted	58	18.8	19.05	97.4
Jakobsbergerholz	47°31'57"N 7°36'10"E	305	44	high	14000	large	fragment	134	17.9	13.54	98.2
Jakobsbergerhölzli	47°31'49"N 7°35'50"E	336	22	medium	21000	large	fragment	134	15.6	13.76	97.6
Lange Erlen	47°34'33"N 7°36'18"E	252	20	medium	21000	large	forest	NA	19.1	12.57	97.9
Linsberg	47°34'25"N 7°39'52"E	425	10	low	50000	large	forest	NA	25.3	20.83	96.9
Matenbühl	47°35'18"N 7°40'10"E	349	3	low	34000	large	forest	NA	23.8	20.18	97.1
Margarethenpark	47°32'31"N 7°35'01"E	301	35	high	19000	large	fragment	136	20.5	13.39	96.1
Mooswaldli	47°34'51"N 7°39'37"E	297	16	medium	4686	medium-sized	fragment	131	27.3	15.14	94.7
Salamanderwegli	47°35'05"N 7°40'09"E	317	8	low	4061	medium-sized	planted	95	23.2	13.57	97.3
Singerstrasse	47°32'49"N 7°36'50"E	276	70	high	1084	small	planted	113	14.9	28.09	98.1
Teich	47°35'12"N 7°38'52"E	275	17	medium	258	small	planted	58	13.9	18.15	93.9
Wenkenköpfl	47°34'29"N 7°39'29"E	372	12	low	36000	large	fragment	131	27.1	23.30	97.8

alter the soil fungal and bacterial community (Baxter et al., 1999; Ossola et al., 2017; Francini et al., 2018), but also the composition of soil invertebrates (earthworms: Smetak et al., 2007; nematodes: Pavao-Zuckerman and Coleman, 2007; Amossé et al., 2016). Recently, there has also been a surge of studies assessing the responses of mites (Rota et al., 2015; Caruso et al., 2017) and springtails to urbanisation with the main focus on air and soil pollution (e.g. Santorufo et al., 2014; Rzeszowski and Sterzyńska, 2016; Sterzyńska et al., 2018). Urban forests are exposed to a wide range of disturbances, which can significantly affect the abundance and species composition of soil/leaf litter invertebrates (Shimano, 2011; Walter and Proctor, 2013). Furthermore, the urban environment and their associated altered abiotic conditions, e.g. higher evapo-transpiration rates (Marzluff et al., 2008), can result in evolutionary selection pressures that allow species with certain morphological and life-history traits to adapt to this novel environment and become so called “urban exploiters” (Faeth et al., 2011; Pickett et al., 2011). For example, urbanisation can reduce the abundance of poorly dispersing ground beetle and rove beetle species (Vergnes et al., 2014), or the abundance of habitat specialists of spiders and isopods (Magura et al., 2008). In contrast, urbanisation caused an increase in more xerophilous and light-preferring ground-dwelling spiders due to the more open warmer habitats in urban areas (Horváth et al., 2012).

Although, there have recently been several studies investigating the influence of urbanisation on litter fauna, leaf litter decomposition processes were rarely examined in urban forests. In our study standardised litterbags were used to examine the impact of urbanisation and forest size on the litter decomposition rates and its associated leaf litter fauna. For this purpose, we exposed litterbags in temperate deciduous forests of different sizes in the city of Basel (Switzerland) and its surroundings for 3, 6 and 9 months. Forests in highly urbanised areas might have an increased soil temperature, which may stimulate macro-decomposer activity (Pouyat and Carreiro, 2003). We therefore expect that the decomposition rate of leaf litter increases with the degree of urbanisation. We also expect that the decomposition rate of leaf litter increases with forest size, because soil moisture stress is more pronounced in smaller forests (more edge per area) than in large forests (Matlack, 1993; Marzluff et al., 2008; Riutta et al., 2012). Soil moisture stress can have a negative impact on microbial decomposer activity reducing decomposition rate (Malmivaara-Lämsä et al., 2008). Furthermore, we expect that the decomposition rate decreases with decreasing mesh size, because of the exclusion of a group of specialised decomposers that can enhance litter decomposition rates (e.g. macrofauna: Slade and Riutta et al., 2012; Remy et al., 2018; mesofauna: Fujii et al., 2018). We hypothesise that decomposition rate increases with degree of urbanisation, but decreases with both forest size and mesh size of the litterbags. Additionally, we hypothesise that the species richness of the litter mesofauna (e.g. Collembola) will decrease in forests located in highly urbanised areas (Korotkevich et al., 2018; Sterzyńska et al., 2018) as well as in small forests due to increased soil disturbances and micro-climatic changes in the litter/soil environment. Furthermore, we expect that the species composition of Collembola in forests situated in highly urbanised areas to shift towards species with greater dispersal abilities (Santorufo et al., 2014).

## 2. Materials and methods

### 2.1. Study area

The study was carried out in the canton of Basel-City, Switzerland (47°34'N, 7°36'E; Fig. 1). The study area covers 37 km<sup>2</sup>, consisting of 26.2 km<sup>2</sup> (70.9 %) residential area, 4.5 km<sup>2</sup> (12.1 %) agricultural land, 4.4 km<sup>2</sup> (11.7 %) forest and 1.7 km<sup>2</sup> (4.5 %) water bodies. The canton of Basel-city has in total 200'408 inhabitants. Basel has an annual precipitation average of 842 mm and annual mean temperature of 10.5 °C.

### 2.2. Study design, forest characteristics and features of the surrounding landscape

To examine the potential effect of the degree of urbanisation and forest area on leaf litter decomposition and their associated fauna, we chose 17 deciduous forests, which differed in degree of urbanisation and ranged in size from 258 m<sup>2</sup> to 50,000 m<sup>2</sup> (Fig. 1; Table 1). Although there are more comprehensive definitions of ‘urban forest’, we considered remnants of former large continuous forests and forests planted after 1884 in nowadays built-up areas as an urban forest. Our definition excludes single trees from streets, industrial places, and urban parks (Randrup et al., 2005; see Table 1 for a detailed description of the forests). The forest sites examined belong to the *Fagetum* association (Burnand and Hasspacher, 1999). However, the forests differ in historical development and consequently in age (Table 1). Thirteen of the forest sites are embedded in a mosaic of settlements, green areas and agricultural lands, while four forest sites are part of large continuous forests measuring more than 40 ha. The most abundant tree species in the tree and shrub layer were European beech (*F. sylvatica*), sycamore (*A. pseudoplatanus*) and ash (*F. excelsior*).

For each forest, land cover data in their surroundings were obtained from satellite images (Google Earth, 2009). The degree of urbanisation was expressed as the percentage cover of sealed area in the surrounding radius of 500 m from the central point of each forest (following Melliger et al., 2017). This was calculated by using the pixel counting function of Adobe Photoshop (version 10.0.1). The degree of urbanisation of the 17 forests examined ranged from 4 to 70 % sealed area (Table 1). A distance of 500 m was chosen to minimise spatial overlap of the surroundings and thus to reduce spatial autocorrelation. Path density (a surrogate for human disturbance) was expressed as the total path length per forest site (in m/ha; Melliger et al., 2017).

In each forest, we set up three randomly chosen sampling plots measuring 4 m × 4 m to assess soil and vegetation characteristics. We applied the Braun-Blanquet scale (Braun-Blanquet, 1964) to determine the species richness of vascular plants and to estimate ground vegetation cover (< 40 cm; for more details see supplementary information of Melliger et al., 2017). We assessed the canopy closure by taking three photographs in each plot and using the pixel counting function of Adobe Photoshop (version 10.0.1). We randomly collected three soil samples in each vegetation plot using a metal cylinder (depth: 5 cm; diameter: 5.05 cm; volume: 100 cm<sup>3</sup>) to assess potential effects of soil characteristics on litter decomposition. We mixed the three soil samples in each plot and then sieved (mesh size 2 mm) and dried them at 50 °C for 96 h. We determined soil moisture content (%) using the fresh to dry ratio. We measured soil temperature using temperature loggers (Thermo button 21 G; software ThermoTrack PC Pro 17) buried at a depth of 2 cm that recorded temperature at an hourly basis during the duration of the incubation period (February–November 2017). In each forest, we assessed soil pH in distilled water (1:2.5 soil:water; Allen, 1989). We determined total soil organic matter content (SOM) as loss-on-ignition of oven-dried soil at 750 °C for 16 h (Allen, 1989). We measured total soil organic nitrogen using the standard method of Kjeldahl (Bremner, 1965).

### 2.3. Litterbags preparation and sampling schedule

Leaf litter decomposition rates were quantified using litterbags with standardised leaves of European beech (*F. sylvatica*), ash (*F. excelsior*), and sycamore (*A. pseudoplatanus*). Recently fallen senescent leaves of each tree species were collected in two forests near Basel in October 2016, cut into 3 cm<sup>2</sup> pieces and subsequently dried at 60 °C for 48 h. Afterwards, we mixed 4.5 g of dried leaves consisting of 1.5 g of each of the three tree species and filled in the litterbags (15 cm × 15 cm). This standardised leaf litter mixture is representative for the natural situation in the forests examined. In this way, we were able to keep litter quality constant (Pouyat et al., 1997). Thus, variation in the

decomposition rate recorded in our study can be attributed to differences in forest characteristics. In order to examine the potential effects of the micro-, meso- and macro-litter fauna on the leaf litter decomposition rate, we used litterbags with three different mesh sizes: small mesh (100  $\mu\text{m}$ ) to exclude the meso- and macro-fauna, medium mesh (2 mm) to exclude the macro-fauna, and large mesh (4 mm) to give access to the micro-, meso-, and macro-fauna (Bradford et al., 2002).

In February 2017, we chose two plots (1 m  $\times$  2 m) for litterbag exposures approximately in the centre of each forest. The two plots were situated 5–50 m (depending on forest size) apart from each other in a homogenous litter matrix to minimise potential effects of different soil and microclimatic conditions. We placed 18 litterbags in six rows consisting of three bags with different mesh size in each plot (36 litterbags per forest, 612 in total). Within each row the order of the bags with different mesh size was randomised. Six litterbags (two of each mesh size) were re-sampled from each plot in May (after 3 months), in August (after 6 months) and in November 2017 (after 9 months). Because some litterbags were removed or vandalised by forest visitors, in a few cases only one litterbag per mesh size was collected per sampling occasion.

#### 2.4. Leaf litter decomposition rate

We used two litterbags of each mesh size from each plot to determine the decomposition rate separately for each mesh size in 3, 6 and 9 months (six bags per plot). After collection, we dried the remaining leaf litter of each bag (60  $^{\circ}\text{C}$  for 48 h) and weighed it. Moisture content of litter (%) was assessed by using the fresh to dry weight ratio of the leaf litter. Because soil contamination was evident in numerous litterbags, oven-dry litter masses were corrected following Blair (1988). We determined leaf litter composition in a total of 518 litterbags (172 bags with 100  $\mu\text{m}$ , 174 bags with 2 mm and 172 bags with 4 mm mesh size).

#### 2.5. Leaf litter fauna extraction and identification

At each sampling occasion (May, August, November 2017), we extracted the leaf litter fauna from four litterbags (two bags with large and medium mesh sizes) in each plot. Following the recommendation of Kampichler and Bruckner (2009), we did not consider the leaf litter fauna in bags with small mesh size (100  $\mu\text{m}$ ). The content of the litterbags were weighed and placed in a Berlese-Tullgren funnel (Van Straalen and Rijninks, 1982) continuously illuminated for 5 days by a 20 W LED lamp. At the end of the extraction procedure, the remaining leaf litter was weighed and the dry leaf litter masses were corrected for soil contamination (see above). In total, the litter fauna was extracted from 188 mesh bags (95 bags with 4 mm and 93 bags with 2 mm). The leaf litter fauna was stored in 70 % ethanol until identification.

Acari were determined to the suborder level (Oribatida, Gamasina, Uropodina, Astigmata, and Prostigmata) using the key of Brohmer (1988). The abundances of these suborders were recorded for each sample. Collembola were determined to the species level following Gisin (1960); Fjellberg (1998, 2007) and Hopkin (2007), species of Tullbergiidae following Dunger and Schlitt (2011), the Symphypleona following Bretfeld (1999), the Isotomidae following Potapov (2001) and the Hypogastruridae following Thibaud et al. (2004). The nomenclature is based on Deharveng (2004). Collembola species were also assigned according to several species traits including maximum body size, body shape, life form/vertical distribution, moisture preference, reproduction mode, leg length, furcula length, and habitat preference using data from the literature (Gisin, 1943, 1960; Salmon et al., 2014; Eilers et al., 2018a,b) and the Digital Repository: <https://doi.org/10.5061/dryad.m6dn0g8>.

#### 2.6. Data analyses

We classified the forests, based on the percentage cover of sealed area in their surroundings, into sites with low (< 15 %), medium (15–30 %) or high (> 30 %) degrees of urbanisation. We also assigned forests to one of three size classes: small (< 4000  $\text{m}^2$ ), medium-sized (4000–10,000  $\text{m}^2$ ) or large (> 10,000  $\text{m}^2$ ) forests (Table 1). We categorised these factors as categorical variables allowing to analyse interactions between variables (see below).

We calculated separately daily litter decomposition rate for the first 3 months, 6 months, and 9 months to obtain estimates for mass loss of litter. To calculate the mean daily decomposition rate ( $k_{\text{litter}}$ ) we applied linear regression, because the litter mass loss was linear over the duration of the incubation period (Wieder and Lang, 1982; Xuluc-Tolosa et al., 2003; Jacob et al., 2010):

$$X_t = -k \cdot t + X_0$$

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 ( $\text{mg g}^{-1} \text{d}^{-1}$ ).

We analysed the data at the site level using the mean of the two plots for each mesh size from each forest. We used generalized linear models (GLM) with quasipoisson distributed errors and log-link function to examine potential effects of the degree of urbanisation and forest size on the decomposition rate ( $k_{\text{litter}}$ ), abundance of total invertebrates, Acari, Oribatida and Collembola, and species richness of Collembola. We used degree of urbanisation and forest size as factors and the forests characteristics (soil moisture, soil organic matter and canopy closure) as cofactors in the GLM models. Other variables were inter-correlated (soil temperature, soil pH, path density, total plant richness, shrub richness, tree richness, cover ground vegetation, cover bare ground) with any of the forest characteristics and thus excluded from the analyses (Table S1a–c). In particular, soil temperature was correlated with soil moisture and path density with degree of urbanisation (Table S1a–c). We also excluded land use history as a factor because it was highly associated with forest area (Kruskal-Wallis-test:  $\chi^2 = 11.2$ ,  $\text{df} = 2$ ,  $P = 0.005$ ). All GLM models were stepwise reduced as recommended by Crawley (2007). All statistical analyses were performed using the software R (R Core Team, 2015, version 3.0.2).

We used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measures to test whether the degree of urbanisation and forest size affected the species composition of Collembola. We applied square-root-transformed data and Wisconsin double standardisation. This transformation standardises species maxima followed by relativisation of sample total. Species that were only recorded in one site or had less than 10 individuals were not included in this analysis.

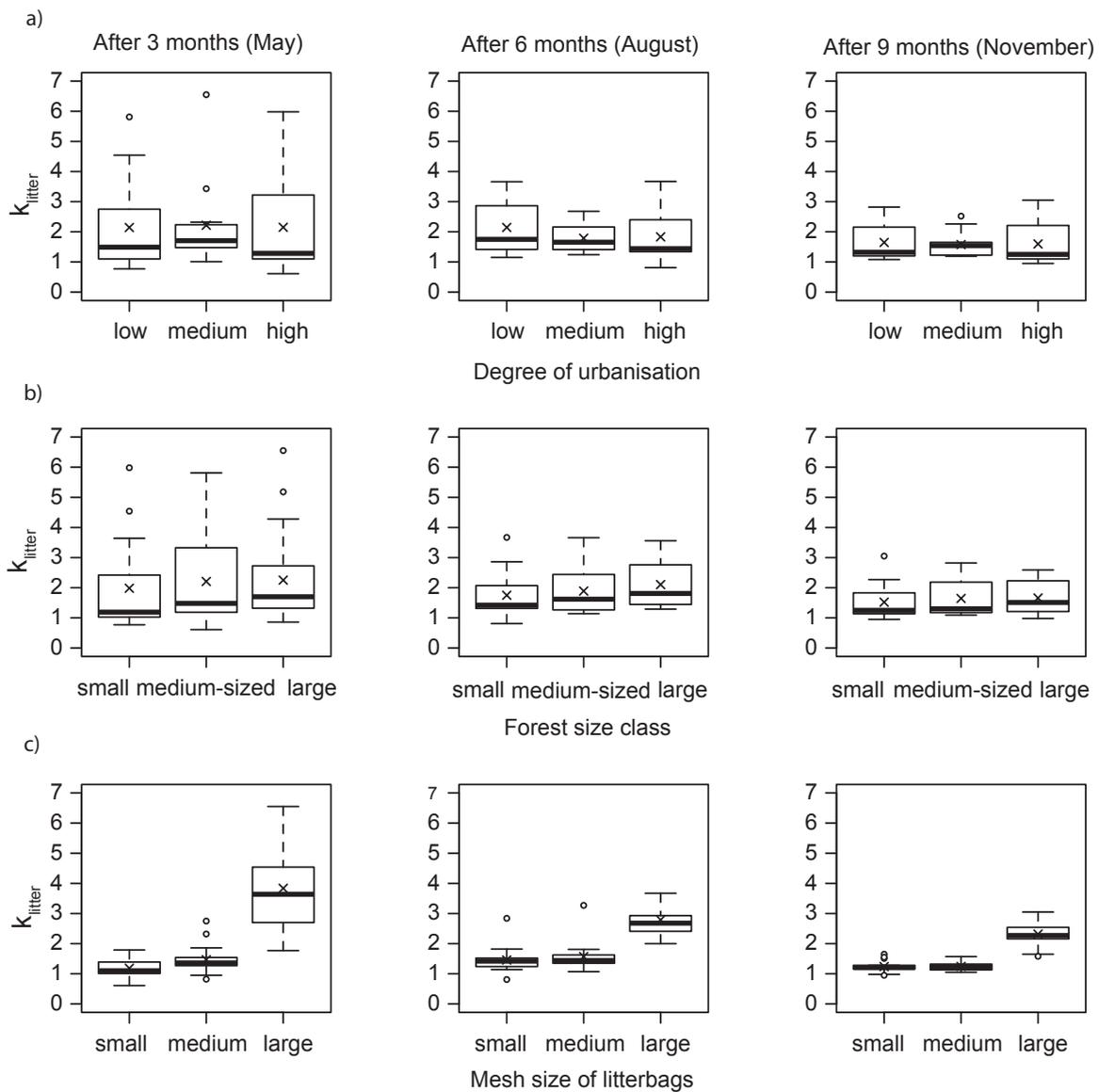
We used permutational multivariate analyses of variance (PERMANOVA) to test whether the degree of urbanisation and forest size influenced Collembola species composition. The PERMANOVA tests were based on 999 permutations of the untransformed raw data with the *vegan* R-package and *adonis* function (Oksanen et al., 2017).

Fourth corner analysis (Dray and Legendre, 2008) was applied to examine the relationship between Collembola species traits and degree of urbanisation, forest size, and the local forest variables soil moisture and soil organic matter content using the *ade4* package in R.

### 3. Results

#### 3.1. Leaf litter decomposition

Leaf litter decomposition rate ( $k_{\text{litter}}$ ;  $\text{mg g}^{-1} \text{d}^{-1}$ ) was differently affected by the degree of urbanisation and forest size during the course of the incubation period (Fig. 2; Tables 2; S2). After 3 and 9 months,  $k_{\text{litter}}$  was not influenced by the degree of urbanisation and forest size (Table 2). However, after 6 months,  $k_{\text{litter}}$  was affected by the degree of urbanisation (Fig. 2), being higher in forests situated in areas with a low



**Fig. 2.**  $K_{litter}$  after 3, 6 and 9 months of incubation in forests situated in areas with different degrees of urbanisation a), different forest sizes b), and litter bags consisting of varying mesh sizes c). The horizontal bars represent medians; the means are represented by an 'x', box ends the first and last quartiles; whiskers the interquartile distance multiplied by 1.5; the open circles indicate outliers.

**Table 2**

Summary of GLM analyses examining the effects of degree of urbanisation, forest size, mesh size of litterbags, soil moisture content (%), soil organic matter content (%), and canopy closure (%) in the forests on the decomposition rate of leaf litter ( $k_{litter}$ :  $mg\ g^{-1}\ d^{-1}$ ).

	$k_{litter}$ after 3 months (May)			$k_{litter}$ after 6 months (August)			$k_{litter}$ after 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,48	0.05	0.960	2,47	3.73	<b>0.033</b>	2,41	0.36	0.699
Forest size	2,46	0.69	0.510	2,45	2.38	0.106	2,39	1.66	0.206
Mesh size	2,44	75.88	<b>&lt; 0.001</b>	2,43	49.35	<b>&lt; 0.001</b>	2,37	105.77	<b>&lt; 0.001</b>
Soil moisture	-	-	-	1,42	5.19	<b>0.028</b>	-	-	-
Soil organic matter	1,43	2.31	0.136	-	-	-	1,36	1.77	0.192
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	-	-	-
Degree of urbanisation* mesh size	4,39	1.02	0.410	4,38	1.12	0.360	4,32	3.29	<b>0.023</b>
Forest size* mesh size	-	-	-	-	-	-	-	-	-

– Factor was excluded from the model due to the step-wise reduction procedure.

Significant effects ( $P < 0.05$ ) are presented in bold.

⊥ Variable removed due to intercorrelation with soil temperature.

degree of urbanisation compared to forests in areas with either a medium or a high degree of urbanisation in their surroundings.

Mesh size significantly influenced the extent of leaf litter decomposition (Fig. 2; Tables 2; S3). After 3, 6 and 9 months, leaf litter decomposition rate was higher in bags with large mesh size than in bags with either medium or small mesh sizes (Fig. 2).  $k_{\text{litter}}$  was similar in mesh bags with medium and small mesh size throughout the incubation period (Fig. 2; Table 2). Furthermore, soil moisture had an effect on  $k_{\text{litter}}$  after 6 months (Table 2). After 9 months, there was a significant interaction between degree of urbanisation and mesh size. Litterbags with large mesh size had the greatest  $k_{\text{litter}}$  in high and low urbanised areas. In contrast, litterbags with both medium and small mesh size had similar  $k_{\text{litter}}$  independent of degree of urbanisation (Tables 2; S2).

### 3.2. Total invertebrates in the leaf litter

A total of 4662 invertebrates comprising of 2926 mites, 1236 springtails and 500 other invertebrates were extracted from the litterbags. After 3 months, 1659 invertebrates (912 mites, 607 springtails and 140 other invertebrates) were recorded, after 6 months, 1323 invertebrates (791 mites, 338 springtails and 194 other invertebrates), and after 9 months 1680 invertebrates (1223 mites, 291 springtails, and 166 other invertebrates). Considering the different mesh sizes, 2819 (60.5 %) invertebrates (1720 mites, 848 springtails and 251 other invertebrates) were extracted from bags with medium mesh size and 1843 (39.5 %) invertebrates (1206 mites, 388 springtails and 249 other invertebrates) from bags with large mesh size (Table S4a, b).

After 3 months, the degree of urbanisation did not affect the abundance of total invertebrates. After 6 and 9 months, however, the abundance of total invertebrates was influenced by the degree of urbanisation (after 6 months:  $F_{2,30} = 8.69$ ,  $P < 0.001$ ; 9 months:  $F_{2,27} = 15.43$ ,  $P < 0.001$ ; Table S5a). In particular, after 6 months the abundance of total invertebrates was higher in forests situated in areas with a high degree of urbanisation (median: 69.5, range: 6–108) than in forests surrounded with a medium (37, 15–92) and a low degree of urbanisation (17, 5–50). After 9 months, the abundance of total invertebrates was higher in forests in medium-urbanised areas (77, 49–220) compared to forests in high (32, 3–77) and low (34, 12–92) urbanised areas. After 9 months abundance was also highest in large forests (65, 9–168) compared to medium-sized (29, 12–87) and small forests (32.5, 3–220;  $F_{2,25} = 3.36$ ,  $P = 0.050$ ; Table S5a).

After 3 and 6 months, mesh size had an influence on the abundance of total invertebrates (after 3 months:  $F_{1,28} = 10.39$ ,  $P = 0.003$ ; 6 months:  $F_{1,27} = 5.64$ ,  $P = 0.025$ ; Table S5a). There was a greater abundance of total invertebrates in litterbags with medium mesh size (after 3 months: 66, 15–128; 6 months: 47, 7–108) compared to litterbags with large mesh size (after 3 months: 28, 4–125; after 6 months: 28, 5–78). An increase in soil organic matter content significantly negatively impacted the abundance of invertebrates (after 3 months:  $F_{1,27} = 5.71$ ,  $P = 0.024$ ;  $r_s = -0.45$ ,  $n = 17$ ,  $P = 0.007$ ; after 9 months:  $F_{1,24} = 5.14$ ,  $P = 0.033$ ; Table S5a).

### 3.3. Acari in the leaf litter

Considering Acari, the Oribatida with 2291 individuals (78.3 %) were the most abundant suborder compared with the Astigmata (315 individuals: 10.8 %), the Gamasina (235: 8.0 %), the Uropodina (62: 2.1 %) and the Prostigmata (23: 0.8 %; Table S4a,b).

The degree of urbanisation affected the total abundance of Acari on all sampling occasions (after 3 months:  $F_{2,31} = 6.46$ ,  $P = 0.005$ ; 6 months:  $F_{2,30} = 3.80$ ,  $P = 0.035$ ; and 9 months:  $F_{2,27} = 26.60$ ,  $P < 0.001$ ; Fig. 3; Table S5b). After 3 months and 9 months, there was a higher abundance of total mites in forests situated in areas with a medium degree of urbanisation than in forests situated in areas with both a low and a high degree of urbanisation in their surroundings, but not after 6 months. After 9 months, forest size affected the abundances

of total Acari ( $F_{2,25} = 6.26$ ,  $P = 0.007$ ; Fig. 4; Table S5b) with lower abundances in medium-sized forests than in small and large-sized forests.

Mesh size affected the abundance of total Acari after 3 months ( $F_{1,28} = 4.87$ ,  $P = 0.036$ ), but not after 6 and 9 months (Table S5b). Bags with medium-sized mesh had the highest abundance of total Acari (33, 8–85) compared to litterbags with large mesh (10, 0–114). After 9 months, the abundance of total Acari was also influenced by canopy closure ( $F_{1,23} = 4.86$ ,  $P = 0.038$ ).

Regarding the various suborders of Acari, the degree of urbanisation impacted the abundance of Oribatida (after 3 months:  $F_{2,31} = 15.00$ ,  $P < 0.001$ ; 6 months:  $F_{2,30} = 3.44$ ,  $P = 0.046$ ; 9 months:  $F_{2,27} = 27.38$ ,  $P < 0.001$ ; Fig. S1; Table S5c). After 3 and 9 months, the highest number of oribatid mites was found in forests situated in areas with a medium degree of urbanisation (3 months: 52, 8–106; and 9 months: 58, 30–196) compared with forests with a low (3 months: 5.5, 0–23; and 9 months: 13, 0–56) and a high degree of urbanisation (3 months: 7.5, 1–44; and 9 months: 12.5, 1–42) in their surroundings. However, after 6 months, there was a slightly higher abundance of Oribatida in forests in highly urbanised areas (18, 0–52) compared to forests in medium (16.5, 4–49) and low (5, 1–37) urbanised areas. Forest size affected the abundance of Oribatida (after 9 months:  $F_{2,25} = 6.51$ ,  $P = 0.006$ ; Fig. S2; Table S5c) being lower in medium-sized forests (9.5, 0–68) than in small (14.5, 1–196) and large-sized forests (43, 5–135). Furthermore, after 9 months, the abundance of Oribatida was affected by canopy closure ( $F_{1,23} = 4.90$ ,  $P = 0.037$ ).

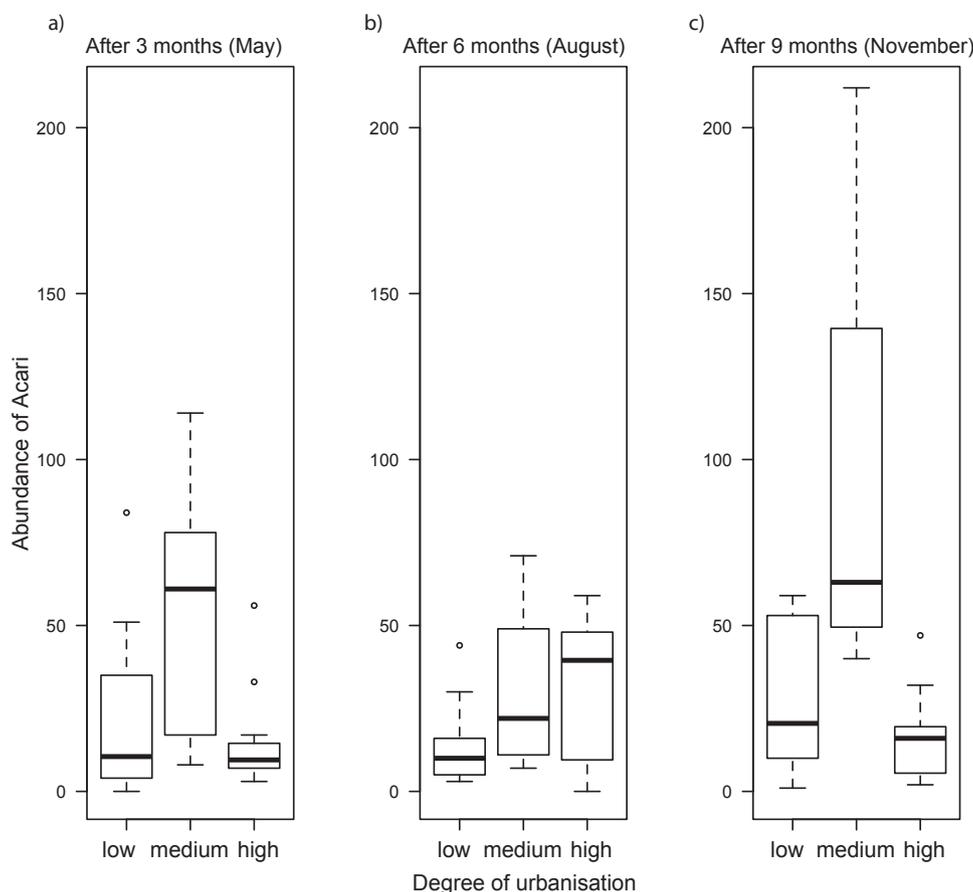
### 3.4. Collembola in the leaf litter

The abundance of Collembola was affected by the degree of urbanisation only after 6 months ( $F_{2,30} = 20.68$ ,  $P < 0.001$ ), but not after 3 and 9 months (Fig. 5; Table S5d). After 6 months, the abundance of Collembola was higher in forests surrounded by dense settlements than in forests situated in areas with medium and low degrees of urbanisation. Forest size affected the abundance of Collembola (after 9 months:  $F_{2,25} = 4.08$ ,  $P = 0.030$ ) with the abundance being highest in large forests compared to medium and small forests (Fig. 6; Table S5d).

Mesh size had an influence on the abundance of Collembola after 3 months ( $F_{1,28} = 16.46$ ,  $P < 0.001$ ) and 6 months ( $F_{1,27} = 18.22$ ,  $P < 0.001$ ; Table S5d). Overall, litterbags with medium-sized mesh had a higher abundance of Collembola (after 3 months: 19, 2–90; 6 months: 7, 0–74) than litterbags with large mesh (3 months: 8, 0–24; 6 months: 2, 0–16). Soil moisture influenced the abundance of Collembola both after 3 and 6 months of incubation (after 3 months:  $F_{1,27} = 5.02$ ,  $P = 0.034$ ; 6 months:  $F_{1,26} = 6.39$ ,  $P = 0.018$ ). Furthermore, after 3 months and 9 months soil organic matter content was affected by the abundance of Collembola. Indeed, after 3 months the abundance of Collembola tended to decrease with increasing soil organic matter content ( $F_{1,26} = 17.48$ ,  $P < 0.001$ ;  $r_s = -0.29$ ,  $n = 17$ ,  $P = 0.090$ ; Table S5d), and was affected by soil organic matter content after 9 months ( $F_{1,24} = 10.90$ ,  $P = 0.003$ ).

As found for abundance, Collembola species richness was affected by the degree of urbanisation after 6 months ( $F_{2,30} = 7.33$ ,  $P = 0.003$ ; Table S6a). Species richness in forests surrounded by a high degree of urbanisation (3.5, 1–5) was on average higher than in forests in medium (2, 0–2) or low urbanised areas (1, 0–4). Furthermore, after 3 months (in May), Collembola species richness tended to be greater in forests with lower soil moisture ( $F_{1,27} = 6.32$ ,  $P = 0.018$ ;  $r_s = -0.31$ ,  $n = 17$ ,  $P = 0.075$ ) and was greater when soil organic matter content was lower (after 3 months:  $F_{1,26} = 7.22$ ,  $P = 0.012$ ;  $r_s = -0.44$ ,  $n = 17$ ,  $P = 0.010$ ). But after 9 months, soil organic matter content had a positive impact on Collembola species richness ( $F_{1,23} = 8.59$ ,  $P = 0.008$ ;  $r_s = 0.38$ ,  $n = 15$ ,  $P = 0.037$ ; Table S6a).

The most frequently recorded Collembola species were *Lepidocyrtus lignorum* with 577 individuals (46.7 %), *Folsomia manolachei* (279; 22.6 %), *Pseudosinella alba* (87; 7.0 %), *Parisetoma notabilis* (78; 6.3 %), and



**Fig. 3.** Abundance of Acari in leaf litter in forests situated in areas with varying degrees of urbanisation during the three sampling periods: a) after 3 months (May), b) after 6 months (August), and c) after 9 months (November). See Fig. 2 for symbols.

*Lepidocyrtus cyaneus* (76; 6.1 %). For more details on the effects of urbanisation and forest size on the recorded Collembola species, see Appendix A in the supplementary material.

### 3.5. Species composition and functional traits of Collembola

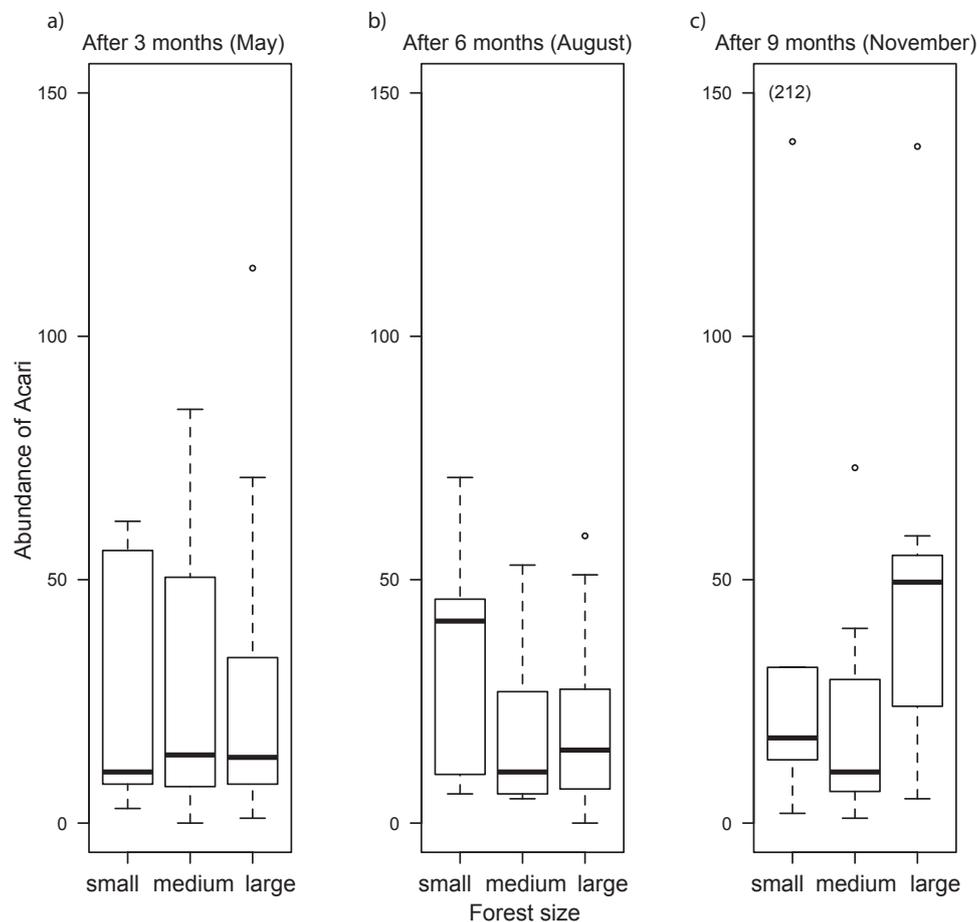
NMDS multivariate analyses and PERMANOVA revealed that neither the degree of urbanisation ( $F_{2,12} = 1.81$ ,  $P = 0.085$ ; Fig. 7) nor forest size ( $F_{2,12} = 0.90$ ,  $P = 0.531$ ; Fig. 8) influenced the species composition of Collembola. Fourth-corner analysis showed that the degree of urbanisation ( $P = 0.005$ ) and forest size ( $P = 0.004$ ) caused a shift in body shape traits. The abundances of both globular and stocky Collembola species were lower in forests surrounded by medium degree of urbanisation than in forests situated in low urbanised areas. Furthermore, globular and stocky collembolans were less abundant in medium-sized forests compared to small forests, and globular collembolans were also more abundant in large forests than in small forests. Life form tended to be affected by forest size, with the life form eudaphic (soil living) being less abundant in small forests than in both medium and large forests ( $P = 0.055$ ; Table S8). In addition, body shape of Collembola was also affected by the soil organic matter content ( $P = 0.025$ ) and the trait leg length tended also to be affected by the soil moisture content ( $P = 0.056$ ; Table S8). Other Collembola species traits (max body size, moisture preference, reproduction mode, furcula length, and habitat preference) were neither affected by the degree of urbanisation nor by forest size (Fig. S3; Tables S7; S8).

## 4. Discussion

### 4.1. Leaf litter decomposition

Leaf litter decomposition rates are in general influenced by several factors including the quality of leaf litter, local environmental conditions of the sites and the different decomposer organisms present (Swift et al., 1979; García-Palacios et al., 2013). The decomposition rate ( $k_{\text{litter}}$ ) found in our study was higher than those reported in other studies considering beech litter in rural deciduous forests in Germany (Jacob et al., 2010) or urban deciduous forests in Basel, Switzerland (Melliger et al., 2017). This discrepancy could be due to the use of leaves from different tree species (Makkonen et al., 2012; Korboulewsky et al., 2016). We assessed the decomposition rate of a leaf litter mixture: two species have easily digestible leaves (*Fraxinus excelsior* and *Acer pseudoplatanus*), while *Fagus sylvatica* has more recalcitrant leaves. Jacob et al. (2010) and Melliger et al. (2017) examined only decomposition of recalcitrant beech leaves. However, any comparison of decomposition rates ( $k_{\text{litter}}$ ) with other studies should be done with caution because of differences in litter types, mesh size of bags, geographic area, habitat type and environmental conditions.

The result that the highest decomposition rate was recorded in forests situated in areas with a low degree of urbanisation contrasts our expectation and the findings of previous studies, which showed a decrease in the decomposition rate along an urban-rural gradient (Pouyat et al., 1997; Pouyat and Carreiro, 2003; Nikula et al., 2010). Other studies conducted in urban parks and gardens postulated that the higher decomposition rates in urban areas are a result of the heat island effect (Pouyat et al., 1997; Pouyat and Carreiro, 2003; Tresch et al., 2019). Although we recorded soil temperature, we focused on the inter-



**Fig. 4.** Abundance of Acari in leaf litter in forests of different sizes during the three sampling periods: a) after 3 months (in May), b) after 6 months (in August), and c) after 9 months (November). The number in brackets is the maximum number of Acari found in mesh bag that did not fit to scale. See Fig. 2 for symbols.

correlated soil moisture, based on the results of a meta-analysis of studies on experimental warming showing that moisture can outweigh the temperature-related influence of leaf litter decomposition rates (Aerts, 2006). Furthermore, a recent study in Italy found that there was no effect of temperature on the decomposition rates in shrublands and forests (Petraglia et al., 2019), while soil moisture content remained important independent of whether litter was considered at the forest edge or interior (Riutta et al., 2012). Even though, microbial decomposer activity can be driven by temperature in environments under intermediate moisture conditions (moisture content ranging from 20 to 80%), in drier/low moisture conditions, increased temperatures can have a negative impact on microbial decomposer activity (Prescott, 2010; Petraglia et al., 2019). In accordance, a study conducted in boreal urban forest fragments in Finland found that the lower moisture of the humus at forest edges was thought to be a major reason for reduced microbial biomass and activity, which could negatively impact decomposition rates (Malmivaara-Lämsä et al., 2008). This could be a reason why we found an effect of soil moisture content on  $k_{litter}$  in forests in low urbanised areas during the warmest part of the year (in August).

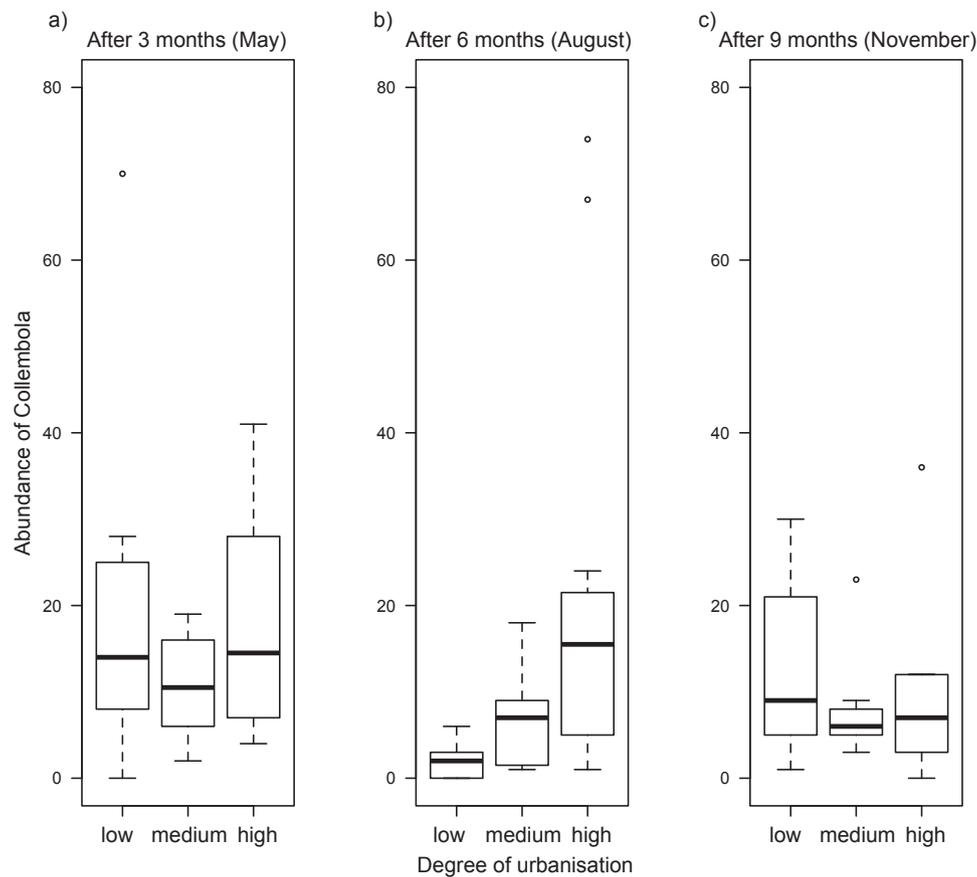
Our result that the size of the forests had no effect on leaf litter decomposition rate contrasts the finding of Melliger et al. (2017), who found a higher decomposition rate of beech leaves in larger forests (which on average had higher soil moisture content) than in medium-sized and small forests. The larger forests in our study also had higher soil moisture contents, so this difference might rather be a result of using different leaf litter types.

In our study, decomposition rate was influenced by mesh size being higher in large (4 mm) than in medium (2 mm) and small (100  $\mu$ m)

mesh litterbags. This result parallels the findings of several studies (e.g. Kampichler and Bruckner, 2009; Riutta et al., 2012; Slade and Riutta, 2012; Bokhorst and Wardle, 2013; Remy et al., 2018), although different reasons were suggested. Kampichler and Bruckner (2009) argued that there was considerable leaching through the larger holes of the litterbags compared to those with finer mesh size, while Riutta et al. (2012); Slade and Riutta (2012); Bokhorst and Wardle (2013), and Remy et al. (2018) found that the greater loss of litter in large mesh litterbags could be attributed to the activity of macro-invertebrates (e.g. ploughing in by earthworms; Cortez and Bouché, 1998). Interestingly, similar decomposition rates were recorded in litterbags with medium and small-sized mesh. Medium-sized mesh litterbags (2 mm) allowed free access for the meso-fauna including mites and Collembola, which are thought to be important decomposers of leaf litter. Therefore, Bradford et al. (2002) expected that the decomposition rate would be higher in medium-sized mesh bags than ones with small mesh size. However, in contrast to this expectation, several studies recorded a weak effect of the soil fauna with similar decomposition rates in medium and small-sized mesh bags as found in the present study (Kampichler and Bruckner, 2009; Bokhorst and Wardle, 2013; García-Palacios et al., 2013; Zhang et al., 2015). Furthermore, it is possible that the small-sized mesh bags change the micro-climate by an increased water retention and a higher light transmittance (Bokhorst and Wardle, 2013), which may enhance the activity of fungi and bacteria (McClougherty and Berg, 2011; Purahong et al., 2016).

#### 4.2. Leaf litter fauna

The leaf litter and soil fauna constitute an important part of the soil



**Fig. 5.** Abundance of Collembola in leaf litter in forests situated in areas with varying degrees of urbanisation: a) after 3 months (in May), b) after 6 months (in August), and c) after 9 months (in November). See Fig. 2 for symbols.

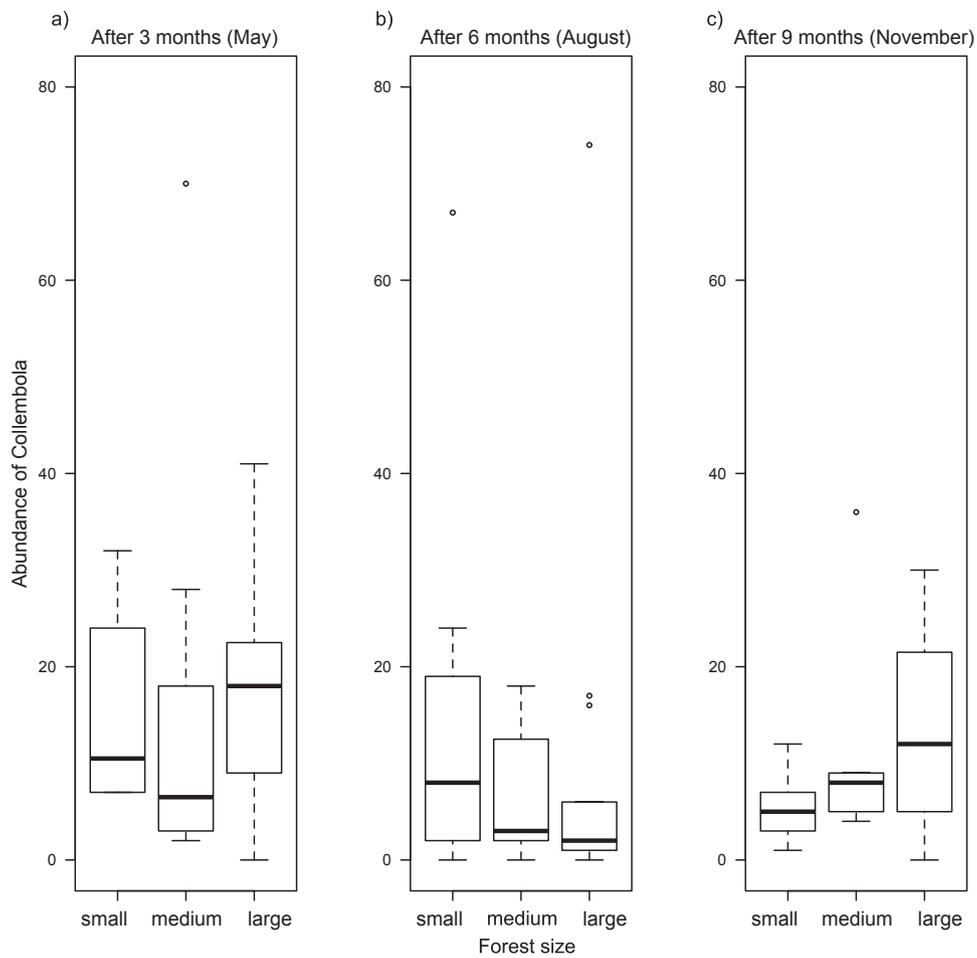
food web and provide key ecosystem services (Wall and Moore, 1999). Soil invertebrates can respond differently to urbanisation (Santorufu et al., 2012). In our study, the degree of urbanisation affected total abundance of Acari being higher in forests situated in areas with moderate levels of urbanisation and even exhibiting greatest abundances in highly urbanised areas in the summer. Several other studies reported a high Acari abundance in urban areas (Santorufu et al., 2012, 2014; Caruso et al., 2017; Mangová et al., 2019). However, these studies on Acari in urban areas were conducted in different habitat types (e.g. lawns) and focused on the effects of pollution (e.g. heavy metal soil pollution, which did not occur in our forests; Gubler et al., 2015). Soil organic matter content was thought to be an important factor for the abundance of oribatids in urban areas (Santorufu et al., 2014), but this soil factor had no influence on the abundance of this group in our study. Coleman et al. (1996) suggested that in disturbed soils (e.g. from anthropogenic activities), the oribatid mite/collembolans ratio should switch from the generally K-strategist oribatid mites to r-strategist collembolans. Concordantly, previous studies found lower densities of oribatid mites in urban areas than suburban areas (Niedbala et al., 1982; Weigmann and Kratz, 1987). However, other more recent studies found high oribatid abundances in urban parks (Caruso et al., 2017) and even in disturbed grasslands close to roads (Santorufu et al., 2014; Rota et al., 2015). We also did not find a negative effect of increasing degree of urbanisation on oribatid abundance. Similar to other studies, the oribatid community we recorded might be fairly tolerant to anthropogenic pressure (Maisto et al., 2017; Mangová et al., 2019).

Considering collembolans, a similar number of species (21 species) was found in our study compared to other leaf litter decomposition studies conducted in urban areas (34 species in Fiera (2009); 22 species in Sterzyńska et al. (2018)). In the present study, collembolan abundance and species richness were highest in forests in areas with a high

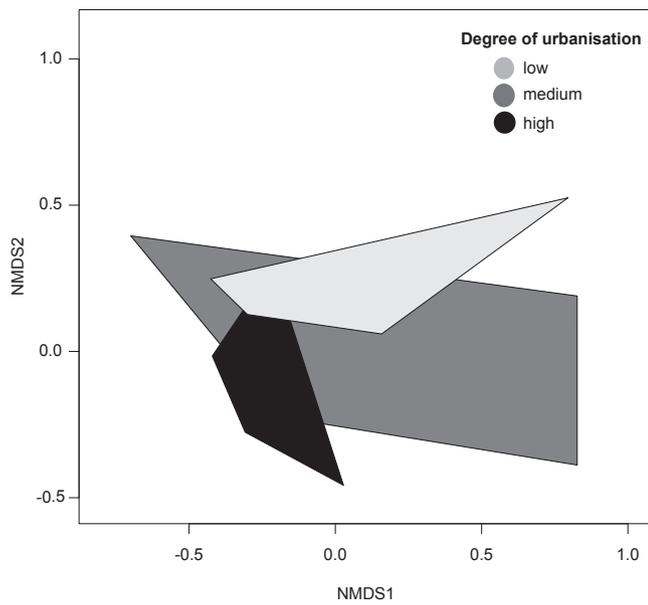
degree of urbanisation. A study conducted in street lawns of Naples, Italy, also found that Collembola species richness was high in soils in urban areas, when there was a thick litter layer and high organic matter content (Santorufu et al., 2014). In our study, we could only partially confirm this relationship, because the impact of soil organic matter content on Collembolan abundance varied throughout the incubation period.

The three Collembola species *Lepidocyrtus lignorum*, *Pseudosinella alba* and *Lepidocyrtus cyaneus* (all belonging to the family Entomobryidae) were the most abundant ones (46.7 %, 7.0 %, and 6.1 %, respectively) in forests situated in areas with a high degree of urbanisation. This could be explained by the high tolerance for soil disturbance of these species, a characteristic feature for the species of this family (Maraun et al., 2003). Anthropogenic disturbances in urban environments can lead to significant changes in belowground trophic niche structure of collembolans, resulting in a reduced interspecific trophic variation (Korotkevich et al., 2018). Some trophic flexible, ubiquitous species such as *L. lignorum* or *L. languinosus* may benefit from the reduced competition in urban areas (Santorufu et al., 2014).

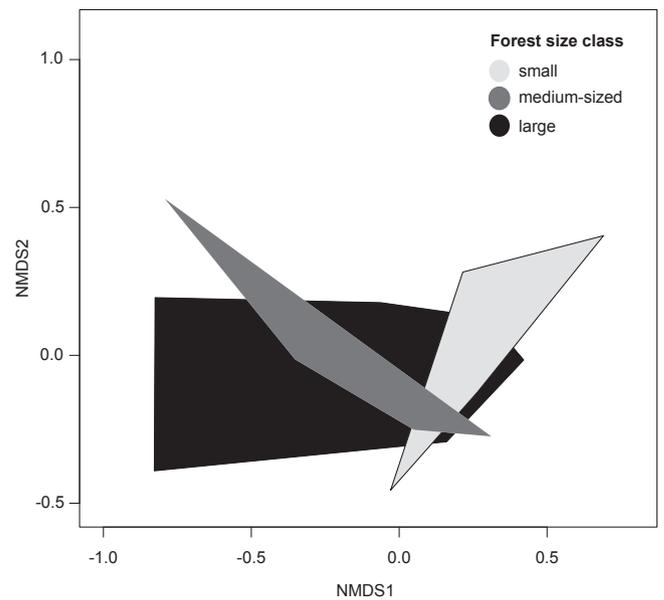
Overall, Acari, Oribatida and collembolan abundances were highest in large forests. This was also true for *F. manolachei*, one of the abundant Collembola species. Individuals of *F. manolachei* were frequently recorded in forests, but the higher abundance in large forests may be due to a preference for higher soil moisture content and driven by resource quantity (thicker litter and soil layer), because this species feeds primarily on plant detritus (Potapov et al., 2014). This forest size effect contrasts a previous study in the Chaco Serrano forest in central Argentina that found no effect of fragment area on the abundance or species richness of soil mesofauna (Moreno et al., 2019). The authors argued that the changes in fragment size were too large in scale to investigate a mesofaunal response, and that the mesofauna was affected



**Fig. 6.** Abundance of Collembola in leaf litter in forests situated in areas with varying degrees of urbanisation: a) after 3 months (in May), b) after 6 months (in August), and c) after 9 months (November). See Fig. 2 for symbols.



**Fig. 7.** NMDS ordination analysis of Collembola species composition in forests located in areas with a low, medium or high degree of urbanisation.



**Fig. 8.** NMDS analyses of Collembola species composition in small, medium-sized and large forests.

by a much smaller spatial (< 20 cm<sup>2</sup> of soil) and temporal scale of soil disturbances and distribution of resources (Rantalainen et al., 2008; Moreno et al., 2019).

In our study, the degree of urbanisation and forest size did not change the collembolan species composition. These findings contrast the studies of Santorufo et al. (2014) and Rzeszowski and Sterzyńska (2016), which reported significant changes in collembolan communities, mainly caused by soil pollution. Because the soils in our forests were not polluted by heavy metals, the environmental stressors may have been less pronounced to force a significant change in collembolan species composition.

Traits of collembolans can be used to describe the distribution of species and impact of environmental variables on their abundance (Vandewalle et al., 2010; Salmon and Ponge, 2012; Salmon et al., 2014). Life form can describe the resource utilisation and dispersal ability of species (Widenfalk et al., 2016). The eudaphic (soil living) collembolans in our study were less abundant in small forests. This could be due to small forests being in environmental conditions more similar to open landscapes (Marzluff et al., 2008). In addition, eudaphic collembolans tend to move to lower depths during the summer when the soil is dry (Detsis, 2000), because they are not able to adjust their physiology during periods of extreme temperatures by increasing the lipid compositions in their bodies as surface-dwelling collembolans do (Van Dooremalen et al., 2013). In contrast, woodlands are characterised by collembolan species with a subterranean (eudaphic) life form, which prefer stable forest sites with high soil moisture and organic matter content (Salmon and Ponge, 2012; da Silva et al., 2016). Forest species with eudaphic life form are also more sensitive to environmental stress such as moisture and temperature fluctuations (Heiniger et al., 2015) and are considered to be less mobile (Salmon and Ponge, 2012). These species might be less capable of adapting to the changing environment and to heterogeneous landscapes with different land use types as surface-dwelling collembolans are (Ponge et al., 2006; Salmon and Ponge, 2012; da Silva et al., 2016).

## 5. Conclusions

Our study showed that urbanisation and forest size impacted the litter fauna and the associated vital ecosystem service of litter decomposition in various ways. We found different responses of mites and Collembola to the degree of urbanisation. Although some frequently recorded Collembola species were positively affected by urbanisation, the species composition of the collembolan community was neither influenced by degree of urbanisation nor by forest size. Our results confirmed findings of other studies that the response of leaf litter and the soil fauna depends on habitat type, the associated local micro-climatic conditions, anthropogenic pressure and species traits.

## Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

## Acknowledgements

We would like to thank the forest owners and foresters in charge for allowing us access to the forests. We thank Brigitte Braschler and two anonymous reviewers for useful comments on the manuscript.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pedobi.2019.150609>.

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## Supplementary material Chapter II

- Table S1** Inter-correlations within and among forest characteristics
- Table S2** Detailed results of GLM analyses on the decomposition rate of leaf litter ( $k_{\text{litter}}$ )
- Table S3** Remaining litter mass (%) in areas of varying degrees of urbanisation and in forests of different size
- Table S4** Abundance of Collembola species, Acari suborders, and other invertebrates in litterbags with different degree of urbanisation, different mesh sizes and sampling periods
- Table S5** Summary of GLM analyses of total invertebrates, Acari, Oribatida, and Collembola
- Table S6** Summary of GLM analyses of Collembola species richness, and Collembola species: *Lepidocyrtus lignorum* and *Folsomia manolachei*
- Appendix A** Analyses of the two most frequently recorded Collembola species
- Table S7** Table of Collembola traits
- Table S8** Fourth-corner statistics for Collembola abundance and environmental variables
- Figure S1** Abundance of Oribatida in leaf litter with varying degrees of urbanisation
- Figure S2** Abundance of Oribatida in leaf litter of different forest sizes
- Figure S3** Fourth-corner analysis of Collembola traits

**Table S1.** Inter-correlations (Spearman's rank correlation) within and among forest characteristics.

<b>a) Forest characteristics in May</b>	
Ground vegetation richness vs. cover of bare ground	$r_s = -0.06, n = 17, P=0.685$
Ground vegetation richness vs. cover of ground vegetation	$r_s = 0.06, n = 17, P=0.678$
Cover ground vegetation vs. canopy closure	$r_s = 0.21, n = 17, P=0.130$
<b>Cover ground vegetation vs. cover bare ground</b>	<b><math>r_s = 0.47, n = 17, P &lt; 0.001</math></b>
Cover bare ground vs. canopy closure	$r_s = 0.27, n = 17, P = 0.055$
Cover bare ground vs. soil organic matter content	$r_s = -0.27, n = 17, P = 0.058$
Cover bare ground vs. soil moisture	$r_s = -0.04, n = 17, P = 0.803$
<b>Canopy closure vs. ground vegetation richness</b>	<b><math>r_s = 0.53, n = 17, P &lt; 0.001</math></b>
Canopy closure vs. shrub richness	$r_s = -0.17, n = 17, P = 0.22$
Canopy closure vs. tree richness	$r_s = -0.09, n = 17, P = 0.53$
<b>Canopy closure vs. total plant richness</b>	<b><math>r_s = 0.45, n = 17, P &lt; 0.001</math></b>
<b>Total plant richness vs soil moisture</b>	<b><math>r_s = 0.46, n = 17, P &lt; 0.001</math></b>
Total plant richness vs soil organic matter content	$r_s = 0.13, n = 17, P = 0.371$
Ground vegetation richness vs. shrub richness	$r_s = 0.03, n = 17, P = 0.84$
<b>Tree richness vs. shrub richness</b>	<b><math>r_s = -0.28, n = 17, P = 0.047</math></b>
<b>Tree richness vs. total plant richness</b>	<b><math>r_s = -0.28, n = 17, P = 0.044</math></b>
<b>Path density vs. sealed area within 500 m</b>	<b><math>r_s = 0.39, n = 17, P = 0.005</math></b>
<b>Path density vs. cover bare ground</b>	<b><math>r_s = 0.37, n = 17, P = 0.008</math></b>
Path density vs. ground vegetation richness	$r_s = -0.21, n = 17, P = 0.149$
<b>Path density vs. total plant richness</b>	<b><math>r_s = -0.32, n = 17, P = 0.024</math></b>
Soil moisture vs. soil organic matter content	$r = 0.19, n = 17, P = 0.173$
Soil moisture vs. soil pH	$r_s = 0.04, n = 17, P = 0.772$
<b>Soil moisture vs. soil temperature</b>	<b><math>r = -0.29, n = 17, P = 0.041</math></b>
<b>Soil moisture vs. canopy closure</b>	<b><math>r_s = 0.39, n = 17, P = 0.004</math></b>
<b>Soil pH vs. soil organic matter content</b>	<b><math>r_s = 0.60, n = 17, P &lt; 0.001</math></b>
Soil temperature vs. canopy closure	$r_s = -0.17, n = 17, P = 0.229$

<b>a) Forest characteristics in May (continued)</b>	
Soil organic matter content vs. canopy closure	$r_s = 0.23, n = 17, P = 0.112$
Soil organic matter vs. path density	$r_s = -0.24, n = 17, P = 0.095$
<b>b) Forest characteristics in August</b>	
Ground vegetation richness vs. cover of bare ground	$r_s = -0.06, n = 15, P = 0.685$
Ground vegetation richness vs. cover of ground vegetation	$r_s = 0.06, n = 17, P = 0.678$
Cover ground vegetation vs. canopy closure	$r_s = 0.21, n = 17, P = 0.130$
<b>Cover ground vegetation vs. cover bare ground</b>	<b><math>r_s = 0.47, n = 17, P &lt; 0.001</math></b>
Cover bare ground vs. canopy closure	$r_s = 0.27, n = 17, P = 0.055$
Cover bare ground vs. soil organic matter content	$r_s = -0.28, n = 17, P = 0.058$
Cover bare ground vs. soil moisture	$r_s = -0.04, n = 17, P = 0.803$
<b>Canopy closure vs. ground vegetation richness</b>	<b><math>r_s = 0.53, n = 17, P &lt; 0.001</math></b>
Canopy closure vs. shrub richness	$r_s = -0.17, n = 17, P = 0.223$
Canopy closure vs. tree richness	$r_s = -0.09, n = 17, P = 0.534$
<b>Canopy closure vs. total plant richness</b>	<b><math>r_s = 0.45, n = 17, P &lt; 0.001</math></b>
<b>Total plant richness vs soil moisture</b>	<b><math>r_s = 0.47, n = 17, P &lt; 0.001</math></b>
Total plant richness vs soil organic matter content	$r_s = 0.13, n = 17, P = 0.371$
Ground vegetation richness vs. shrub richness	$r_s = 0.28, n = 17, P = 0.843$
<b>Tree richness vs. shrub richness</b>	<b><math>r_s = 0.28, n = 17, P = 0.047</math></b>
<b>Tree richness vs. total plant richness</b>	<b><math>r_s = -0.28, n = 17, P = 0.045</math></b>
<b>Path density vs. sealed area within 500 m</b>	<b><math>r_s = 0.39, n = 17, P = 0.005</math></b>
<b>Path density vs. cover bare ground</b>	<b><math>r_s = 0.37, n = 17, P = 0.008</math></b>
Path density vs. ground vegetation richness	$r_s = -0.20, n = 17, P = 0.149$
<b>Path density vs. total plant richness</b>	<b><math>r_s = -0.31, n = 17, P = 0.024</math></b>
Soil moisture vs. soil organic matter content	$r_s = 0.19, n = 17, P = 0.173$
Soil moisture vs. soil pH	$r_s = 0.04, n = 17, P = 0.772$
<b>Soil moisture vs. soil temperature</b>	<b><math>r_s = -0.29, n = 17, P = 0.041</math></b>
<b>Soil moisture vs. canopy closure</b>	<b><math>r_s = 0.40, n = 17, P = 0.004</math></b>

**b) Forest characteristics in August (continued)**

<b>Soil pH vs. soil organic matter content</b>	<b><math>r_s = 0.60, n = 17, P &lt; 0.001</math></b>
soil temperature vs. canopy closure	$r_s = -0.17, n = 17, P = 0.229$
soil organic matter content vs. canopy closure	$r_s = 0.23, n = 17, P = 0.112$
Soil organic matter vs. path density	$r_s = -0.24, n = 17, P = 0.095$

**c) Forest characteristics in November**

Ground vegetation richness vs. cover of bare ground	$r_s = 0.22, n = 15, P=0.144$
<b>Ground vegetation richness vs. cover of ground vegetation</b>	<b><math>r_s = 0.48, n = 15, P=0.001</math></b>
<b>Cover ground vegetation vs. canopy closure</b>	<b><math>r_s = 0.44, n = 15, P=0.003</math></b>
<b>Cover ground vegetation vs. cover bare ground</b>	<b><math>r_s = 0.31, n = 15, P = 0.042</math></b>
<b>Cover bare ground vs. canopy closure</b>	<b><math>r_s = 0.54, n = 15, P &lt; 0.001</math></b>
Cover bare ground vs. soil organic matter content	$r_s = -0.15, n = 15, P = 0.319$
Cover bare ground vs. soil moisture	$r_s = 0.17, n = 15, P = 0.265$
<b>Canopy closure vs. ground vegetation richness</b>	<b><math>r_s = 0.51, n = 15, P &lt; 0.001</math></b>
Canopy closure vs. shrub richness	$r_s = -0.09, n = 15, P = 0.552$
Canopy closure vs. tree richness	$r_s = -0.09, n = 15, P = 0.565$
<b>Canopy closure vs. total plant richness</b>	<b><math>r_s = 0.43, n = 15, P = 0.004</math></b>
<b>Total plant richness vs soil moisture</b>	<b><math>r_s = 0.42, n = 15, P = 0.005</math></b>
Total plant richness vs soil organic matter content	$r_s = 0.05, n = 15, P = 0.726$
<b>Ground vegetation richness vs. shrub richness</b>	<b><math>r_s = 0.42, n = 15, P = 0.004</math></b>
Tree richness vs. shrub richness	$r_s = 0.01, n = 15, P = 0.955$
Tree richness vs. total plant richness	$r_s = -0.08, n = 15, P = 0.608$
Path density vs. sealed area within 500 m	$r_s = 0.10, n = 15, P = 0.529$
Path density vs. cover bare ground	$r_s = 0.18, n = 15, P = 0.242$
Path density vs. ground vegetation richness	$r_s = 0.16, n = 15, P = 0.283$
Path density vs. total plant richness	$r_s < -0.01, n = 15, P = 0.999$
Soil moisture vs. soil organic matter content	$r_s = 0.06, n = 15, P = 0.723$
Soil moisture vs. soil pH	$r_s = 0.04, n = 15, P = 0.813$

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**c) Forest characteristics in November (continued)**

<b>Soil moisture vs. soil temperature</b>	<b><math>r_s = -0.61, n = 15, P &lt; 0.001</math></b>
Soil moisture vs. canopy closure	$r_s = 0.25, n = 15, P = 0.098$
<b>Soil pH vs. soil organic matter content</b>	<b><math>r_s = 0.68, n = 15, P &lt; 0.001</math></b>
soil temperature vs. canopy closure	$r_s = -0.27, n = 15, P = 0.097$
soil organic matter content vs. canopy closure	$r_s = 0.15, n = 15, P = 0.331$
Soil organic matter vs. path density	$r_s = -0.12, n = 15, P = 0.441$

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**Table S2.** Detailed results of GLM analyses examining the effects of degree of urbanisation, forest size, mesh size of litterbags, soil moisture content (%), soil organic matter content (%), canopy closure (%) in the forests on the decomposition rate of leaf litter ( $k_{\text{litter}}$ :  $\text{mg g}^{-1} \text{d}^{-1}$ ).

	$k_{\text{litter}}$ after 3 months (May)				$k_{\text{litter}}$ after 6 months (August)				$k_{\text{litter}}$ after 9 months (November)			
	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>
(Intercept)	1.70	0.38	<b>4.44</b>	<b>&lt;0.001</b>	0.58	0.23	2.50	<b>0.018</b>	0.94	0.19	4.88	<b>&lt;0.001</b>
Urbanisation low	-0.12	0.17	-0.72	0.479	-0.07	0.11	-0.59	0.557	-0.03	0.08	-0.41	0.682
Urbanisation medium	-0.27	0.19	-1.41	0.169	-0.17	0.13	-1.27	0.214	-0.23	0.09	-2.48	<b>0.020</b>
Forestsize class 2	0.07	0.19	-1.41	0.169	0.05	0.13	0.41	0.687	0.09	0.09	0.94	0.358
Forestsize class 3	-0.05	0.17	-0.31	0.759	0.06	0.12	0.55	0.587	0.03	0.09	0.31	0.761
Mesh size medium	-1.34	0.28	-4.7	<b>&lt;0.001</b>	-0.75	0.16	-4.70	<b>&lt;0.001</b>	-0.69	0.11	-6.38	<b>&lt;0.001</b>
Mesh size small	-1.47	0.30	-4.88	<b>&lt;0.001</b>	-0.83	0.16	-5.05	<b>&lt;0.001</b>	-0.81	0.11	-7.12	<b>&lt;0.001</b>
Soil moisture	0.01	0.01	0.53	0.601	0.02	0.01	2.17	<b>0.037</b>	<0.01	0.01	0.44	0.665
Soil organic matter	-0.02	0.013	-1.53	0.135	0.01	0.01	0.58	0.566	-0.01	0.01	-1.09	0.285
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	⊥	⊥	-0.01	0.02	-0.07	0.943
Urbanisation low: mesh size medium	0.23	0.31	0.74	0.464	0.23	0.19	1.21	0.232	0.05	0.14	0.39	0.700
Urbanisation medium: mesh size medium	0.41	0.35	1.17	0.249	0.28	0.21	1.22	0.203	0.31	0.14	2.16	<b>0.040</b>
Urbanisation low: mesh size small	0.18	0.34	0.53	0.600	0.13	0.9	0.67	0.507	0.17	0.14	1.15	0.262
Urbanisation medium: mesh size small	0.56	0.37	1.53	0.135	0.34	0.21	1.59	0.121	0.43	0.15	2.87	<b>0.008</b>

	k <sub>litter</sub> after 3 months (May)				k <sub>litter</sub> after 6 months (August)				k <sub>litter</sub> after 9 months (November)			
	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t value</i>	<i>P</i>
Forest size medium: mesh size medium	-0.02	0.32	-0.04	0.965	-0.08	0.22	-0.37	0.714	-0.12	0.15	-0.79	0.438
Forest size large: mesh size medium	0.37	0.33	1.15	0.260	0.09	0.19	0.46	0.647	0.01	0.13	0.12	0.920
Forest size medium: mesh size small	-0.03	0.41	-0.06	0.949	-0.12	0.23	-0.52	0.605	-0.02	0.15	-0.12	0.904
Forest size large: mesh size small	0.17	0.35	0.48	0.631	0.14	0.20	0.74	0.466	0.03	0.14	0.19	0.853

⊥ Variable not considered due to correlation with other variable.

**Table S3.** Remaining litter mass (%) after 3, 6, and 9 months. Means  $\pm$  SE are given for three different litterbag mesh sizes in forests situated in areas of varying degrees of urbanisation and in forests of different size.

	Remaining litter mass (%)			Remaining litter mass (%)			Remaining litter mass (%)		
	after 3 months (May)			after 6 months (August)			after 9 months (November)		
	Small mesh	Medium mesh	Large mesh	Small mesh	Medium mesh	Large mesh	Small mesh	Medium mesh	Large mesh
Degree of urbanisation									
low	89.1 $\pm$ 1.1	85.2 $\pm$ 2.3	63.7 $\pm$ 4.5	74.2 $\pm$ 1.7	70.9 $\pm$ 1.0	48.8 $\pm$ 3.7	64.7 $\pm$ 1.9	66.2 $\pm$ 1.9	33.2 $\pm$ 3.6
medium	85.4 $\pm$ 1.7	84.2 $\pm$ 2.1	66.9 $\pm$ 10.1	72.1 $\pm$ 1.9	72.3 $\pm$ 2.1	56.5 $\pm$ 2.7	61.7 $\pm$ 3.0	63.4 $\pm$ 2.1	44.9 $\pm$ 6.6
high	90.4 $\pm$ 0.8	88.0 $\pm$ 0.8	60.6 $\pm$ 4.7	76.4 $\pm$ 2.0	74.9 $\pm$ 1.5	47.8 $\pm$ 4.5	70.1 $\pm$ 1.6	66.8 $\pm$ 1.4	32.7 $\pm$ 3.9
Forest size									
small	90.3 $\pm$ 0.6	89.3 $\pm$ 1.0	63.9 $\pm$ 6.4	76.8 $\pm$ 2.3	74.8 $\pm$ 1.8	51.5 $\pm$ 5.5	68.9 $\pm$ 1.5	66.9 $\pm$ 1.3	38.1 $\pm$ 6.8
medium-sized	88.6 $\pm$ 2.1	87.2 $\pm$ 1.0	60.5 $\pm$ 5.6	76.1 $\pm$ 2.6	72.2 $\pm$ 1.4	47.1 $\pm$ 5.5	64.3 $\pm$ 2.4	66.9 $\pm$ 1.4	32.8 $\pm$ 4.3
large	87.7 $\pm$ 1.2	83.2 $\pm$ 1.8	64.4 $\pm$ 5.3	72.2 $\pm$ 1.1	71.6 $\pm$ 1.4	51.1 $\pm$ 2.9	64.0 $\pm$ 3.3	63.9 $\pm$ 2.0	36.6 $\pm$ 4.0

**Table S4a.** Abundance of Collembola species, Acari suborders and other invertebrates in leaf litterbags exposed in forests of different size (small, medium-size and large) and surrounded by different degrees of urbanisation (low, medium and high).

Invertebrate group/species	Family	Urbanisation gradient			Forest size		
		low	medium	high	small	medium-sized	large
<i>Choreutinula inermis</i>	Hypogastruridae	2	0	0	1	0	1
<i>Friesea mirabilis</i>	Neanuridae	2	5	0	5	2	0
<i>Neanura muscorum</i>	Neanuridae	3	1	9	9	0	4
<i>Kalaphorura burmeisteri</i>	Onychiuridae	0	9	3	0	9	3
<i>Onychiurus</i> sp.	Onychiuridae	0	0	1	0	0	1
<i>Desoria violacea</i>	Isotomidae	0	1	0	0	0	1
<i>Folsomia manolachei</i>	Isotomidae	128	77	74	61	71	147
Isotomidae juvenile	Isotomidae	0	0	1	0	1	0
<i>Parisotoma notabilis</i>	Isotomidae	20	12	46	17	13	48
<i>Entomobrya</i> juvenile	Entomobryidae	0	0	1	0	1	0
Entomobryidae juvenile	Entomobryidae	2	1	13	11	2	3
<i>Lepidocyrtus cyaneus</i>	Entomobryidae	11	9	56	19	8	49
<i>Lepidocyrtus lanuginosus</i>	Entomobryidae	1	0	0	0	1	0
<i>Lepidocyrtus lignorum</i>	Entomobryidae	166	62	349	140	145	292
<i>Lepidocyrtus paradoxus</i>	Entomobryidae	0	1	0	1	0	0
<i>Lepidocyrtus</i> juvenile	Entomobryidae	6	2	7	11	0	4
<i>Orchesella flavescens</i>	Entomobryidae	5	5	4	7	1	6
<i>Pogonognathellus flavescens</i>	Entomobryidae	1	0	0	0	0	1

Invertebrate group/species	Family	Urbanisation gradient			Forest size		
		low	medium	high	small	medium-sized	large
<i>Pseudosinella alba</i>	Entomobryidae	9	13	65	43	4	40
<i>Tomocerus baudoti</i>	Tomoceridae	0	0	1	0	0	1
Tomoceridae juvenile	Tomoceridae	3	0	1	0	2	2
Neelidae juvenile	Neelidae	2	1	0	1	1	1
<i>Dicyrtoma fusca</i>	Dicyrtomidae	7	1	2	9	1	0
<i>Sminthurinus aureus</i>	Katiannidae	13	3	6	14	1	7
<i>Arrhopalites pygmaeus</i>	Arrhopalitidae	9	0	1	1	1	8
Symphyleona juvenile	-	2	1	0	2	0	1
Acari suborders							
Oribatida	-	467	1259	565	876	350	1065
Gamasina	-	65	79	91	93	57	85
Uropodina	-	27	6	29	17	11	34
Astigmata	-	184	72	59	108	117	90
Prostigmata	-	4	16	3	5	6	12
Other invertebrates							
Woodlice (Isopods)	-	10	52	47	33	49	27
Millipedes (Diplopoda)	-	2	4	25	22	1	8
Snails (Gastropoda)	-	7	7	13	0	10	17
Earthworms (Annelida)	-	6	0	1	0	2	5
Aphids (Aphidoidea)	-	2	3	0	5	0	0
Psyllids (Psyllidae)	-	1	4	0	4	1	0

Invertebrate group/species	Family	Urbanisation gradient			Forest size		
		low	medium	high	small	medium-sized	large
Other invertebrates							
Psyllids (Psyllidae)	-	1	4	0	4	1	0
Leafhoppers (Cicadellidae)	-	1	0	0	0	0	1
Moths (Lepidoptera) larvae	-	12	1	0	0	0	13
Flies (Diptera) larvae	-	42	18	47	56	20	31
Thrips (Thysanoptera)	-	3	3	1	1	2	4
Rove beetles (Staphylinidae)	-	0	2	1	0	3	0
Other beetles (Coleoptera)	-	13	7	13	12	10	11
Centipedes (Myriapoda)	-	1	4	13	4	3	11
Pseudoscorpions (Pseudoscorpiones)	-	32	11	18	16	16	29
Ants (Formicidae)	-	3	0	22	7	1	17
Wasps (other Hymenoptera)	-	6	5	8	11	6	2
Spiders (Araneae)	-	11	5	13	9	7	13

**Table S4b.** Abundance of Collembola species, Acari suborders and other invertebrates in litterbags with medium (2 mm) and large (4 mm) mesh in forests at the three sampling periods after 3 months (May), 6 months (August), and 9 months (November).

Invertebrate group/species		After 3 months (May)		After 6 months (August)		After 9 months (November)	
Collembola species	Family	Medium mesh	Large mesh	Medium mesh	Large mesh	Medium mesh	Large mesh
<i>Choreutinula inermis</i>	Hypogastruridae	1	0	1	0	0	0
<i>Friesea mirabilis</i>	Neanuridae	0	0	1	0	3	3
<i>Neanura muscorum</i>	Neanuridae	0	0	6	1	3	3
<i>Kalaphorura burmeisteri</i>	Onychiuridae	0	0	1	0	7	4
<i>Onychiurus</i> sp.	Onychiuridae	1	0	0	0	0	0
<i>Desoria violacea</i>	Isotomidae	1	0	0	0	0	0
<i>Folsomia manolachei</i>	Isotomidae	41	18	59	25	93	43
Isotomidae juvenile	Isotomidae	0	1	0	0	0	0
<i>Parisotoma notabilis</i>	Isotomidae	24	9	14	8	8	15
<i>Entomobrya</i> juvenile	Entomobryidae	1	0	0	0	0	0
Entomobryidae juvenile	Entomobryidae	10	2	2	0	0	2
<i>Lepidocyrtus cyaneus</i>	Entomobryidae	14	10	28	13	7	4
<i>Lepidocyrtus lanuginosus</i>	Entomobryidae	0	1	0	0	0	0
<i>Lepidocyrtus lignorum</i>	Entomobryidae	273	104	125	13	20	42
<i>Lepidocyrtus paradoxus</i>	Entomobryidae	0	0	0	0	1	0
<i>Lepidocyrtus</i> juvenile	Entomobryidae	0	6	5	4	0	0

Invertebrate group/species		After 3 months (May)		After 6 months (August)		After 9 months (November)	
Collembola species	Family	Medium mesh	Large mesh	Medium mesh	Large mesh	Medium mesh	Large mesh
<i>Orchesella flavescens</i>	Entomobryidae	6	4	1	3	0	0
<i>Pogonognathellus flavescens</i>	Entomobryidae	0	1	0	0	0	0
<i>Pseudosinella alba</i>	Entomobryidae	46	4	19	6	7	5
<i>Tomocerus baudoti</i>	Tomoceridae	0	1	0	0	0	0
Tomoceridae juvenile	Tomoceridae	0	1	0	0	1	2
Neelidae juvenile	Neelidae	1	0	0	1	1	0
<i>Dicyrtoma fusca</i>	Dicyrtomidae	0	8	0	0	1	1
<i>Sminthurinus aureus</i>	Katiannidae	9	8	1	0	1	3
<i>Arrhopalites pygmaeus</i>	Arrhopalitidae	0	0	0	0	3	7
Symphyleona juvenile	-	0	1	1	0	0	1
<b>Acari suborders</b>							
Oribatida	-	383	247	310	267	599	485
Gamasina	-	70	36	28	29	33	39
Uropodina	-	5	1	18	7	12	19
Astigmata	-	147	22	89	38	12	7
Prostigmata	-	1	0	3	2	10	7
<b>Other invertebrates</b>							
Woodlice (Isopods)	-	1	26	33	29	2	18
Millipedes (Diplopoda)	-	22	1	2	2	4	0

Invertebrate group/species		After 3 months (May)		After 6 months (August)		After 9 months (November)	
Other invertebrates	Family	Medium mesh	Large mesh	Medium mesh	Large mesh	Medium mesh	Large mesh
Snails (Gastropoda)	-	0	2	10	0	0	15
Earthworms (Annelida)	-	0	0	3	0	0	4
Aphids (Aphidoidea)	-	0	2	0	3	0	0
Psyllids (Psyllidae)	-	5	0	0	0	0	0
Leafhoppers (Cicadellidae)	-	0	0	0	1	0	0
Moths (Lepidoptera) larvae	-	0	0	4	7	1	1
Flies (Diptera) larvae	-	10	8	27	16	32	14
Thrips (Thysanoptera)	-	2	0	0	0	2	3
Rove beetles (Staphylinidae)	-	1	1	0	1	0	0
Other beetles (Coleoptera)	-	5	4	6	8	7	3
Centipedes (Myriapoda)	-	5	5	4	0	4	0
Pseudoscorpions (Pseudoscorpiones)	-	12	7	8	11	16	7
Ants (Formicidae)	-	1	7	0	0	0	17
Wasps (other Hymenoptera)	-	0	2	6	2	6	3
Spiders (Araneae)	-	2	9	3	8	5	2

**Table S5a.** Summary of GLM analyses examining the effects of the degree of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the total number of invertebrates in the leaf litter.

	Abundance of total invertebrates								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	2.10	0.142	2,30	8.69	<b>&lt;0.001</b>	2,27	15.43	<b>&lt;0.001</b>
Forest size	2,29	0.03	0.972	2,28	0.47	0.631	2,25	3.36	<b>0.050</b>
Mesh size	1,28	10.39	<b>0.003</b>	1,27	5.64	<b>0.025</b>	–	–	–
Soil moisture	–	–	–	–	–	–	–	–	–
Soil organic matter	1,27	5.71	<b>0.024</b>	–	–	–	1,24	5.14	<b>0.033</b>
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	1,23	3.69	0.067

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S5b.** Summary of GLM analyses examining the effects of the degree of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the abundance of Acari in the leaf litter

	Abundance of Acari								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	6.46	<b>0.005</b>	2,30	3.80	<b>0.035</b>	2,27	26.60	<b>&lt;0.001</b>
Forest size	2,29	0.19	0.828	2,28	0.90	0.418	2,25	6.26	<b>0.007</b>
Mesh size	1,28	4.87	<b>0.036</b>	1,27	1.28	0.269	–	–	–
Soil moisture	–	–	–	–	–	–	–	–	–
Soil organic matter	–	–	–	–	–	–	1,24	2.93	0.101
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	1,23	4.86	<b>0.038</b>

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S5c.** Summary of GLM analyses examining the effects of the degree of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the abundance of Oribatida in the leaf litter.

	Abundance of Oribatida								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	15.00	<b>&lt;0.001</b>	2,30	3.44	<b>0.046</b>	2,27	27.38	<b>&lt;0.001</b>
Forest size	2,29	0.87	0.430	2,28	0.33	0.719	2,25	6.51	<b>0.006</b>
Mesh size	1,28	2.54	0.123	-	-	-	-	-	-
Soil moisture	1,27	3.59	0.069	-	-	-	-	-	-
Soil organic matter	1,26	2.20	0.150	-	-	-	1,24	1.31	0.265
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	1,23	4.90	<b>0.037</b>

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S5d.** Summary of GLM analyses examining the effects of the degree of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the abundance of Collembola in the leaf litter.

	Abundance of Collembola								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	3.22	0.056	2,30	20.68	<b>&lt;0.001</b>	2,27	1.00	0.383
Forest size	2,29	2.00	0.156	2,28	0.21	0.815	2,25	4.08	<b>0.030</b>
Mesh size	1,28	16.46	<b>&lt;0.001</b>	1,27	18.22	<b>&lt;0.001</b>	–	–	–
Soil moisture	1,27	5.02	<b>0.034</b>	1,26	6.39	<b>0.018</b>	–	–	–
Soil organic matter	1,26	17.48	<b>&lt;0.001</b>	–	–	–	1,24	10.90	<b>0.003</b>
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	–	–	–

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S6a.** Summary of GLM analyses examining the effects of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the species richness of Collembola in the leaf litter.

	Collembola species richness								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	0.08	0.926	2,30	7.33	<b>0.003</b>	2,27	0.32	0.727
Forest size	2,29	1.37	0.271	2,28	0.06	0.940	2,25	0.04	0.957
Mesh size	1,28	1.83	0.187	1,27	3.75	0.063	1,24	1.39	0.250
Soil moisture	1,27	6.32	<b>0.018</b>	-	-	-	-	-	-
Soil organic matter	1,26	7.22	<b>0.012</b>	-	-	-	1,23	8.59	<b>0.008</b>
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	-	-	-

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Appendix A: Analyses of the two most frequently recorded Collembola species. Continued from Results 3.4. Collembola in the leaf litter.**

*L. lignorum* was influenced by the degree of urbanisation after 6 months in August ( $F_{2,30} = 10.08$ ,  $P < 0.001$ ; Table S6b). Its abundance was highest in forests in areas with a high degree of urbanisation (mean  $\pm$  SE  $10.3 \pm 5.0$ ) compared to forests situated in areas with low ( $0.4 \pm 0.2$ ) and medium degrees of urbanisation ( $1.1 \pm 0.7$ ). After 3, 6 and 9 months, *F. manolachei* was influenced by the degree of urbanisation (after 3 months:  $F_{2,31} = 5.73$ ,  $P = 0.008$ ; 6 months:  $F_{2,30} = 5.17$ ,  $P = 0.013$ ; 9 months:  $F_{2,27} = 6.18$ ,  $P = 0.008$ ; Table S6c). After 3 and 9 months, *F. manolachei* abundance was highest in areas with low (after 3 months:  $3.0 \pm 0.7$ ; 9 months:  $7.6 \pm 2.3$ ) than medium (3 months:  $0.9 \pm 0.4$ ; 9 months:  $4.1 \pm 2.5$ ) and high (3 months:  $0.8 \pm 0.5$ ; 9 months:  $2.3 \pm 0.7$ ) degrees of urbanisation. Whereas, after 6 its abundance was higher in forests in areas with a medium degree of urbanisation ( $4.6 \pm 2.1$ ) compared to forests situated in areas with high ( $3.1 \pm 1.8$ ) and medium degrees of urbanisation ( $0.8 \pm 0.4$ ).

Forest size influenced the abundance of *F. manolachei* (after 9 months:  $F_{2,25} = 9.58$ ,  $P = 0.001$ ; Table S6c). *F. manolachei* had a higher abundance in large forests ( $8.1 \pm 2.3$ ) than in medium-sized forests ( $3.1 \pm 1.0$ ) and small forests ( $1.4 \pm 0.7$ ). Furthermore, mesh size had a significant effect on the abundances of *L. lignorum* (after 3 months:  $F_{1,28} = 9.77$ ,  $P = 0.004$ , 6 months:  $F_{1,27} = 12.08$ ,  $P = 0.002$ ; Table S6b). After 3 months, the abundance of *L. lignorum* was also affected by soil organic matter ( $F_{1,27} = 10.67$ ,  $P = 0.003$ ; Table S6b). Considering *F. manolachei*, mesh size affected its abundance after 3 months ( $F_{1,28} = 4.86$ ,  $P = 0.036$ ), 6 months ( $F_{1,27} = 4.35$ ,  $P = 0.047$ ), and 9 months ( $F_{1,24} = 6.75$ ,  $P = 0.017$ ; Table S6c). Litterbags with medium mesh size had a higher abundance of *F. manolachei* (after 3 months:  $2.4 \pm 0.7$ ; 6 months:  $3.7 \pm 1.6$ ; 9 months:  $6.2 \pm 1.9$ ) than litterbags with large mesh (after 3 months:  $1.1 \pm 0.3$ ; 6 months:  $1.5 \pm 0.7$ ; 9 months:  $2.9 \pm 1.0$ ). The abundance of *F. manolachei* was tended to be positively affected by soil moisture content ( $F_{1,26} = 18.25$ ,  $P < 0.001$ ;  $r_s = 0.30$ ,  $n = 17$ ,  $P = 0.091$ ) only after 6 months (in August).

**Table S6b.** Summary of GLM analyses examining the effects of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the abundance of the most common collembolan species *Lepidocyrtus lignorum*.

	Abundance of <i>L. lignorum</i>								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	2.31	0.118	2,30	10.08	<b>&lt;0.001</b>	2,27	2.22	0.132
Forest size	2,29	2.62	0.091	2,28	0.53	0.594	2,25	2.88	0.077
Mesh size	1,28	9.77	<b>0.004</b>	1,27	12.08	<b>0.002</b>	1,24	1.25	0.274
Soil moisture	-	-	-	1,26	3.69	0.066	-	-	-
Soil organic matter	1,27	10.67	<b>0.003</b>	-	-	-	1,23	3.28	0.083
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	-	-	-

- Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S6c.** Summary of GLM analyses examining the effects of urbanisation, forest size, mesh size, soil moisture content (%), soil organic matter content (%), and canopy closure on the abundance of *Folsomia manolachei*.

	Abundance of <i>F. manolachei</i>								
	After 3 months (May)			After 6 months (August)			After 9 months (November)		
	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
Degree of urbanisation	2,31	5.73	<b>0.008</b>	2,30	5.17	<b>0.013</b>	2,27	6.18	<b>0.008</b>
Forest size	2,29	1.27	0.299	2,28	2.70	0.086	2,25	9.58	<b>0.001</b>
Mesh size	1,28	4.86	<b>0.036</b>	1,27	4.35	<b>0.047</b>	1,24	6.75	<b>0.017</b>
Soil moisture	1,27	1.15	0.292	1,26	18.25	<b>&lt;0.001</b>	1,23	1.88	0.184
Soil organic matter	-	-	-	-	-	-	1,22	3.35	0.081
Canopy closure	⊥	⊥	⊥	⊥	⊥	⊥	1,21	1.10	0.306

- Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

⊥ Variable not considered due to correlation with other variable.

**Table S7.** Collembola traits

Collembola species	Microhabitat		Reproduction mode		Locomotory organs		Habitat preference	
	Max body size (mm)	Body shape	Life form	Moisture preference	Leg length	Furcula length		
<i>Arrhopalites pygmaeus</i>	0.5	globular	eu.	4	sex.	long	long	forest
<i>Dicyrtoma fusca</i>	2	globular	ep.	3	sex.	long	long	forest
<i>Folsomia manolachei</i>	1	slender	hemi.	3	sex.	short	short	meadow
<i>Friesea mirabilis</i>	1.9	slender	hemi.	3	sex.	short	absent	both
<i>Kalaphorura burmeisteri</i>	1.2	slender	eu.	5	sex.	short	absent	both
<i>Lepidocyrtus cyaneus</i>	1.5	slender	ep.	4	sex.	long	long	meadow
<i>Lepidocyrtus lignorum</i>	2	slender	ep.	2	sex.	long	long	both
<i>Neanura muscorum</i>	3.5	stocky	hemi.	4	parth.	short	absent	forest
<i>Orchesella flavescens</i>	5	slender	ep.	3	sex.	long	absent	forest
<i>Parisotoma notabilis</i>	1	slender	hemi.	3	parth.	long	long	both
<i>Pseudosinella alba</i>	1.1	slender	hemi.	3	parth.	long	long	meadow
<i>Sminthurinus aureus</i>	1	globular	ep.	5	sex.	long	long	meadow

Max body size: (mm) <sup>1,2,3</sup>

Body shape: very slender, slender, globular, or stocky<sup>2</sup>

Life form/vertical distribution: ep. = epedaphic (surface living); hemi. = hemiedaphic (sub-surface living); eu. = eudaphic (soil living).<sup>2,3</sup>

Moisture preference: 1: xerophilous; 2: xero-mesophilous; 3: mesophilous; 4: hygro-mesophilous; 5: hygrophilous.<sup>1</sup>

Reproduction mode: sex. = sexual; parth. = parthogenetic.<sup>1</sup>

Leg length: Short legs (leg III/body < 0.3); 2 = Long legs (leg III/body ≥ 0.3).<sup>2</sup>

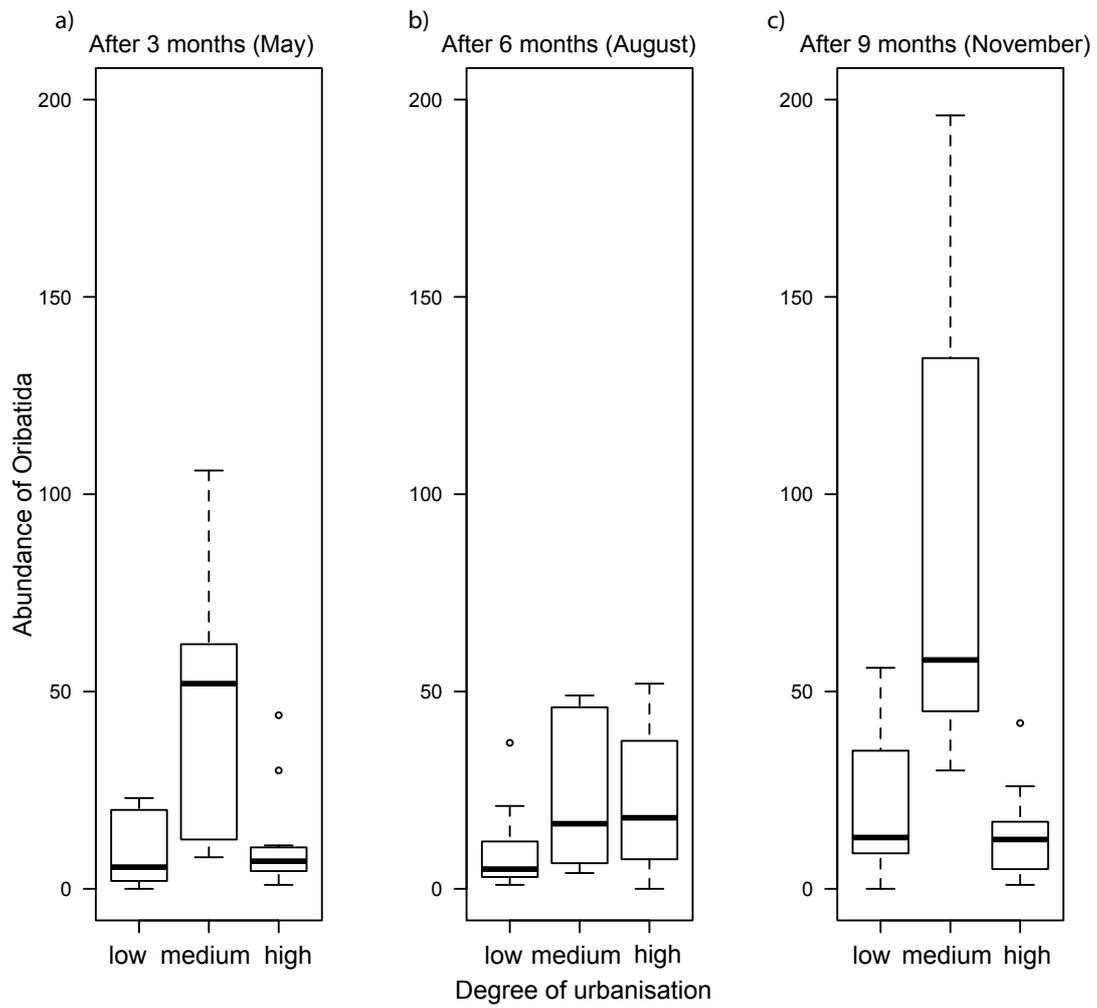
Furcula length: absent= Furcula absent or vestigial; short = Short furcula (anterior part of Abd II not reached); long = Long furcula (anterior part of Abd II reached).<sup>2</sup>

Habitat preference: forest = mainly forest; meadow = mainly meadow; both = occur in meadow and forest habitats.<sup>4,5</sup>

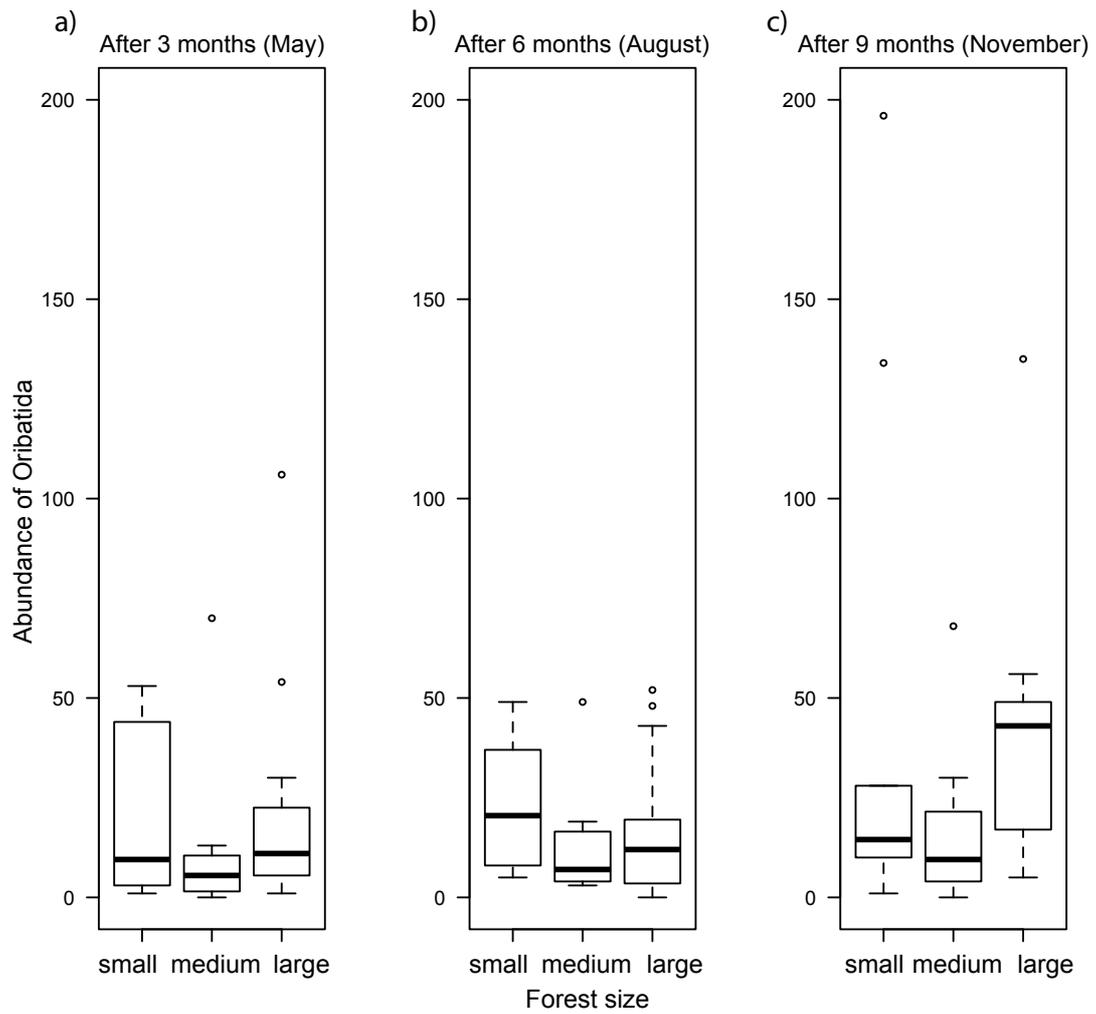
Sources: <sup>1</sup> Ellers et al. (2018), <sup>2</sup>Salmon et al. (2014), <sup>3</sup>Salamon (personal communication), <sup>4</sup>Gisin (1943), <sup>5</sup>Gisin (1960)

**Table S8.** Fourth-corner statistics for Collembola abundance showing the combination of each environmental variable (degree of urbanisation, forest size, soil moisture and soil organic matter) and each Collembola trait.

1	fores.l / max_body_size	0.469811695	-0.12564546	less	0.367	
2	fores.m / max_body_size	0.145705104	-0.38528344	less	0.371	
3	fores.s / max_body_size	0.381094029	0.45295109	less	0.684	
4	urban.h / max_body_size	0.407083217	-0.50284009	less	0.367	
5	urban.l / max_body_size	0.350071735	0.38622547	less	0.66	
6	urban.m / max_body_size	0.226182081	0.48591820	less	0.8	
7	soil_moisture / max_body_size	-0.129713482	-0.91157812	two-sided	0.386	
8	Soil_SOM / max_body_size	-0.029195202	-0.41175379	two-sided	0.769	
9	<b>fores.l / body_shape</b>	<b>0.334349363</b>	<b>-2.18342857</b>	<b>less</b>	<b>0.045</b>	*
10	<b>fores.m / body_shape</b>	<b>0.032906916</b>	<b>-2.24977979</b>	<b>less</b>	<b>0.004</b>	**
11	fores.s / body_shape	0.605700172	3.16210720	less	0.99	
12	urban.h / body_shape	0.486300334	0.08904715	less	0.528	
13	urban.l / body_shape	0.418609332	1.27329949	less	0.939	
14	<b>urban.m / body_shape</b>	<b>0.086764061</b>	<b>-1.71294492</b>	<b>less</b>	<b>0.005</b>	**
15	Soil_moisture / body_shape	-0.097730352	-0.61381554	two-sided	0.651	
16	<b>soil_SOM / body_shape</b>	<b>0.158249126</b>	<b>1.96181841</b>	<b>two-sided</b>	<b>0.025</b>	*
17	fores.l / life_form	0.509289120	0.25343521	less	0.518	
18	fores.m / life_form	0.247541344	1.61856788	less	0.971	
19	fores.s / life_form	0.243097790	-1.24337532	less	0.055	.
20	urban.h / life_form	0.429807044	-0.57530243	less	0.31	
21	urban.l / life_form	0.332521220	0.48495744	less	0.646	
22	urban.m / life_form	0.189726285	0.25706406	less	0.623	
23	soil_moisture / life_form	0.108069488	0.85378950	two-sided	0.495	
24	Soil_SOM / life_form	0.123557423	1.49370142	two-sided	0.117	
25	fores.l / moisture_preference	0.476449826	-0.44417819	less	0.263	
26	fores.m / moisture_preference	0.211055555	0.76771383	less	0.738	
27	fores.s / moisture_preference	0.304118579	-0.22803967	less	0.488	
28	urban.h / moisture_preference	0.502598366	0.23057510	less	0.584	
29	urban.l / moisture_preference	0.304860497	0.02897084	less	0.48	
30	urban.m / moisture_preference	0.173127564	-0.28465314	less	0.44	
31	soil_moisture / moisture_preference	-0.043238853	-0.28989757	two-sided	0.847	
32	Soil_SOM / moisture_preference	0.048878790	0.59319131	two-sided	0.646	
33	fores.l / reproduction_mode	0.515572479	0.35270441	less	0.665	
34	fores.m / reproduction_mode	0.104924216	-0.98217921	less	0.195	
35	fores.s / reproduction_mode	0.359314359	0.24109606	less	0.727	
36	urban.h / reproduction_mode	0.638528383	1.22691934	less	0.924	
37	urban.l / reproduction_mode	0.193403533	-1.16776295	less	0.127	
38	urban.m / reproduction_mode	0.149201129	-0.63094123	less	0.182	
39	soil_moisture / reproduction_mode	-0.184030397	-1.24676206	two-sided	0.21	
40	Soil_SOM / reproduction_mode	0.056269241	0.72263502	two-sided	0.536	
41	fores.l / leg_length	0.500199006	0.06335630	less	0.27	
42	fores.m / leg_length	0.242979517	1.24932867	less	0.975	
43	fores.s / leg_length	0.251515318	-0.93268426	less	0.066	.
44	urban.h / leg_length	0.322496894	-1.47348994	less	0.103	
45	urban.l / leg_length	0.373078807	0.96114149	less	0.871	
46	urban.m / leg_length	0.213775253	0.77586359	less	0.887	
47	soil_moisture / leg_length	-0.212304071	-1.64142690	two-sided	0.056	.
48	Soil_SOM / leg_length	-0.131202111	-1.57999002	two-sided	0.103	
49	fores.l / furcula_length	0.430877489	-1.33783569	less	0.087	.
50	fores.m / furcula_length	0.241449491	1.36130378	less	0.978	
51	fores.s / furcula_length	0.323937758	0.14604220	less	0.683	
52	urban.h / furcula_length	0.345195410	-1.43472438	less	0.107	
53	urban.l / furcula_length	0.315055510	0.18840807	less	0.478	
54	urban.m / furcula_length	0.252309016	2.09320203	less	0.966	
55	soil_moisture / furcula_length	-0.127086455	-1.01704886	two-sided	0.399	
56	Soil_SOM / furcula_length	-0.124249068	-1.51770745	two-sided	0.123	
57	fores.l / habitat_preference	0.478166450	-0.70735708	less	0.209	
58	fores.m / habitat_preference	0.165343886	-0.32939702	less	0.377	
59	fores.s / habitat_preference	0.336777708	0.57109817	less	0.745	
60	urban.h / habitat_preference	0.454019819	-0.33023237	less	0.419	
61	urban.l / habitat_preference	0.359394614	1.10934083	less	0.854	
62	urban.m / habitat_preference	0.158500022	-0.80841474	less	0.232	
63	soil_moisture / habitat_preference	-0.008263271	-0.06916283	two-sided	0.958	
64	Soil_SOM / habitat_preference	-0.126564990	-1.61057657	two-sided	0.083	.



**Fig. S1.** Abundance of Oribatida in leaf litter exposed in forests situated in areas with varying degrees of urbanisation during the three sampling periods a) after 3 months (in May), b) after 6 months (in August), c) after 9 months (November).



**Fig. S2.** Abundance of Oribatida in leaf litter exposed in forests of different sizes during the three sampling periods a) after 3 months (in May), b) after 6 months (in August), c) after 9 months (November).

	Forest size			Degree of urbanisation			soil moisture	soil organic matter
	large	medium -sized	small	high	low	medium		
max body size								
body shape								
life form								
moisture preference								
reproduction mode								
leg length								
furcula length								
habitat preference								

**Fig. S3.** Fourth-corner analysis of Collembola traits in forests situated in areas with different degree of urbanisation and of different size classes. ( $P > 0.05$  was shown).



## Chapter III

### **Saproxyllic insects and fungi in deciduous forests along a rural-urban gradient**

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*Ecology and Evolution*, 2021, 11(4): 1634–1652

# Saproxylic insects and fungi in deciduous forests along a rural–urban gradient

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## Funding information

Basler Stiftung für experimentelle Zoologie;  
Basler Stiftung für Biologische Forschung;  
Emilia Guggenheim-Schnurr Stiftung

## Abstract

Urbanization is increasing worldwide and is regarded a major threat to biodiversity in forests. As consequences of intensive human use, the vegetation structure of naturally growing urban forests and their amount of deadwood can be reduced. Deadwood is an essential resource for various saproxylic insects and fungi. We assessed the effects of urbanization and forest characteristics on saproxylic insects and fungi. We exposed standardized bundles consisting of each three freshly cut beech and oak branches in 25 forests along a rural–urban gradient in Basel (Switzerland). After an exposure of 8 months, we extracted the saproxylic insects for 10 months using an emergence trap for each bundle. We used drilling chips from each branch to determine fungal operational taxonomic units (OTUs). In all, 193,534 insect individuals emerged from the experimental bundles. Our study showed that the abundance of total saproxylic insects, bark beetles, longhorn beetles, total flies, moths, and ichneumonid wasps decreased with increasing degree of urbanization, but not their species richness. However, the taxonomic composition of all insect groups combined was altered by wood moisture of branches and that of saproxylic beetles was influenced by the degree of urbanization. Unexpectedly, forest size and local forest characteristics had a minor effect on saproxylic insects. ITS (internal transcribed spacer of rDNA) analysis with fungal specific primers revealed a total of 97 fungal OTUs on the bundles. The number of total fungal OTUs decreased with increasing degree of urbanization and was affected by the volume of naturally occurring fine woody debris. The composition of fungal OTUs was altered by the degree of urbanization and pH of the branch wood. As a consequence of the altered compositions of saproxylics, the association between total saproxylic insects and fungi changed along the rural–urban gradient. Our study shows that urbanization can negatively impact saproxylic insects and fungi.

## KEYWORDS

beetles, fine woody debris, flies, forest size, urbanization

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## 1 | INTRODUCTION

Urbanization is increasing globally and is considered a major driver of environmental change (Grimm et al., 2008). The expansion of built-up areas reduces the size of natural and seminatural areas and increases their spatial isolation (McKinney, 2006). Several studies reported alterations in abiotic conditions in remaining habitat patches (e.g., increased temperature and N deposition) from the rural surroundings to the city center (Pickett et al., 2011). These changes influence habitat quality and, consequently, the species richness, species composition, and functional diversity of plants and arthropods, which in turn affect the functioning of ecosystems (McDonnell & Hahs, 2015; Merckx & Van Dyck, 2019). Furthermore, urbanization can influence the population dynamics of animals and plants by altering the distribution and abundance of hosts, pathogens, and vectors (Meineke et al., 2013; Moreira et al., 2019).

Urban forests, which can be either remnants of former continuous forests, actively planted, or a result of ongoing succession, are among the most frequent type of green areas in cities (Cvejić et al., 2015). Urban forests provide a wide range of ecosystem services for residents, from areas for recreation, to the recycling and storage of nutrients, air filtering and temperature regulation, and habitat for native species (Escobedo et al., 2011). In general, temperate broad-leaved forests in Europe have been more heavily impacted compared to any other forest biome (Hannah et al., 1995). Naturally growing urban forests can vary in intensity of recreational activities and maintenance measures (New, 2015). As a result of intensive management, the forest structure can be reduced and biodiversity can decline (Lonsdale et al., 2008). In many cases, this results in a reduced amount of deadwood, the essential resource for deadwood-dependent (saproxylic) organisms (Müller & Bütler, 2010; Ódor et al., 2006). A diverse array of organisms including arthropods and fungi depend on deadwood. Deadwood is assumed to be important for 20%–30% of forest species in northern Europe (Stokland et al., 2012). Saproxylic arthropods fill various functional roles, from breaking down the deadwood substrate (xylophages and saprophages) to preying on other saproxylic organisms or parasitizing potential timber pest species (Ulyshen & Šobotnik, 2018). Wood-inhabiting fungi can have multiple interactions with other saproxylic organisms, e.g., allowing access to fresh deadwood by detoxifying plant defenses and/or by providing nutrition (Birkemoe et al., 2018). Several saproxylic insects are associated with wood-decaying fungi (Biedermann & Vega, 2020) or even dependent on a particular fungal species for nutrition (Birkemoe et al., 2018; Floren et al., 2015; Jonsell & Nordlander, 2004). Together, these saproxylic organisms (invertebrates, fungi, bacteria and other microbes) accelerate the decay process of deadwood and are important for carbon sequestration, nutrient recycling, and overall biodiversity in the forests (Parisi et al., 2018; Stokland et al., 2012; Ulyshen, 2016).

Beside the amount of deadwood, the decay stage and deadwood quality are measures of resource availability for saproxylic organisms and suitable indicators for the biodiversity of arthropods (Lassauce et al., 2011; Müller & Bütler, 2010). Physical–chemical

properties (e.g., lignin content, wood pH, moisture content) of deadwood (Hoppe et al., 2016), different decay stages, and the diameter of deadwood can affect the diversity of saproxylic organisms (Brin et al., 2011; Schiegg, 2001). In addition, saproxylic diversity is affected by local microclimatic factors such as temperature and humidity that are influenced by canopy openness and exposure to sunlight (Müller et al., 2020; Seibold et al., 2016).

Studies that assessed the impact of urbanization on arthropods along a rural–urban gradient yielded contrasting results. Some studies reported high abundances of several arthropod groups in urban areas (herbivorous arthropods: Raupp et al., 2010). Other studies, however, found a decline in the abundance and/or species richness of several arthropod groups from the rural surroundings to the city center (butterflies and moths: Merckx & Van Dyck, 2019; Diptera: Nelson & Forbes, 2014; Theodorou et al., 2020; carabid beetles: Niemelä & Kotze, 2009; Piano et al., 2020; parasitoid wasps: Fenoglio & Salvo, 2010; Nelson & Forbes, 2014; overall terrestrial arthropods: Piano et al., 2020). However, knowledge about the potential impact of urbanization on saproxylic organisms is scarce. Some studies investigated the microhabitat of tree hollows in veteran trees in urban parks and found a high diversity of saproxylic beetles in Helsinki (Peuhu et al., 2019) and the presence of endangered beetles (e.g., *Osmoderma eremita*) in Rome (Carpaneto et al., 2010). However, to our knowledge, no study investigated so far the potential effects of urbanization on the overall saproxylic insect community and fungi along a rural–urban gradient.

We used a standardized sampling procedure to examine whether the degree of urbanization, forest size, and/or local forest characteristics (including naturally occurring deadwood and branch characteristics) affected the communities of saproxylic insects and fungi. We exposed bundles consisting of freshly cut oak (*Quercus robur*) and beech (*Fagus sylvatica*) branches in 25 broad-leaved forests along a rural–urban gradient in the city of Basel (Switzerland) and its surroundings for 8 months and subsequently collected the saproxylic insects in emergence traps for 10 months. In particular, our study aimed to assess: (1) the number of total saproxylic individuals (saproxylic beetles, flies, moths, and parasitic wasps) emerging from the deadwood bundles; (2) the taxonomic richness of beetles, flies, and moths; (3) the proportion of saproxylic individuals belonging to different ecological feeding guilds; (4) the proportion of the taxonomic richness of various feeding guilds; and (5) the taxon composition of all saproxylic insects that emerged, and in particular that of the beetles.

We also assessed whether (6) the number of fungal operational taxonomic units (OTUs) and (7) their composition on the bundles were influenced by the degree of urbanization, forest size, local forest characteristics, and branch characteristics. Finally, we examined whether (8) there exist fungal OTU–saproxylic insect associations on the bundles exposed.

We expected that an increase in the degree of urbanization and reduction in forest size both negatively affected the species richness and abundance of saproxylic insects because many species of these groups might be sensitive to forest fragmentation and

habitat isolation, altered environmental conditions, and a reduced amount of deadwood in isolated urban forests (Lassauce et al., 2011; Schiegg, 2001). In contrast, we expected pioneer saproxylic beetles to be less affected by an increase in degree of urbanization and reduction in forest size because many of them are excellent flyers (e.g., bark beetles; Gossner et al., 2013; Komonen & Müller, 2018). Similar to related (albeit nonsaproxylic) insects like carabid beetles (Niemelä & Kotze, 2009), flies (Avondet et al., 2003), and moths (Piano et al., 2020), we expected the taxonomic composition to shift with urbanization. We also expected some local habitat variables such as resource availability (deadwood amount) to positively affect saproxylic individuals (Schiegg, 2001; Seibold et al., 2015) and that microclimatic variables (e.g., wood moisture content of the bundles exposed) influenced saproxylic insect richness and abundance (Vanderwel et al., 2006). Regarding saproxylic fungi, we expected a reduction in fungal OTUs with increasing degree of urbanization, decreasing forest size, and decreasing percentage forest area in the surroundings, because the microclimatic conditions are altered in small urban forest fragments; in particular, temperatures are higher and humidity lower (Bässler et al., 2010; New, 2015), and there is reduced amount of deadwood (Lonsdale et al., 2008). In turn, we expected a decrease in the proportion of mycetophagous and saprophagous insects with increasing degree of urbanization and decreasing forest size because of the reduced diversity of fungi or decayed wood material, which they feed on (Birkemoe et al., 2018; Vanderwel et al., 2006). Many saproxylic insects have strong preferences for specific deadwood-decaying fungi (Biederman & Vega, 2020; Floren et al., 2015); therefore, we expected to find associations between taxonomic composition of insects and fungal OTUs.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was carried out in the city of Basel and its surroundings (northwestern Switzerland; 47°34'N, 7°36'E, elevation: 245–565 m a.s.l.). There are approximately 200,000 residents living in Basel city with a population density around 5,000 inhabitants per km<sup>2</sup> (www.bfs.admin.ch). The study area covers 88.3 km<sup>2</sup>, consisting of 43.6 km<sup>2</sup> (49.4%) residential area, 16.1 km<sup>2</sup> (18.3%) agricultural land, 25.5 km<sup>2</sup> (28.8%) forest, 2.2 km<sup>2</sup> (2.5%) water bodies, and 0.9 km<sup>2</sup> (1.0%) other. In the study area, the total annual precipitation averages 842–1,005 mm and annual mean temperature 10.2–10.9°C (records from 1981 to 2010, www.meteoswiss.admin.ch).

To examine the potential effect of urbanization and forest size on saproxylic fauna, we chose 25 broad-leaved forests that ranged in size from 0.1084 ha to 359.0 ha along an urbanization gradient (Table S1). The forests 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. Ten of these forests are remnants of former large continuous forests (fragments), and four forests were planted after

1884, while six forests are part of larger forests (>40 ha). The remaining five forests are situated in the rural surroundings and were part of large, beech-dominated forests (>52.0 ha; Table S1; Figure S1). Management of the forests (time since last thinning and management intensity) was similar among the forests investigated. The most abundant tree species in these forests are European beech (*Fagus sylvatica*), sycamore (*Acer pseudoplatanus*), European oak (*Quercus robur*), ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), and Norway maple (*Acer platanoides*). The ground vegetation in the forests has a high richness of vernal geophytes including *Anemone nemorosa*, *Ranunculus ficaria*, *Polygonatum multiflorum*, and *Arum maculatum*.

In each forest, we selected an area dominated by deciduous trees (60%–90% of all tree individuals). This investigation area (hereafter forest site) was defined as the polygon determined by the six adult trees on which the bundles were attached (see below). The investigation area varied in size from 0.1 ha to 2.88 ha because some forests were extremely small and the distance between adult trees varied strongly among sites (Table S1). We assessed the degree of urbanization of each forest site, expressed as the percentage cover of sealed area within a radius of 500 m around the center of each forest site, using satellite images (Google Earth, 2009, 2020; Kanton Basel-Landschaft, <https://www.geoview.bl.ch/>) and the pixel counting function of Adobe Photoshop (version 10.0.1). The degree of urbanization of the 25 forest sites examined ranged from 0% to 70% sealed area (Table S1).

### 2.2 | Exposure of deadwood bundles in the field

To assess species richness and abundance of saproxylic insects, we used a slightly modified version of the method developed by Müller et al. (2015). In each forest site, we exposed six tree branch bundles as bait for saproxylic insects. The bundles were tied to a tree at a height of 1.5 m above ground (Figure S2). To avoid effects of heterogeneous microclimatic and weather conditions, all bundles were attached to the south side of a beech or oak tree located in closed canopy stands. The distance between the bundles ranged from 5 to 80 m. The bundles consisted of six freshly cut branches, three each of beech (*Fagus sylvatica*) and oak (*Quercus robur*) (branch length: 80 cm; diameter: 1.5–7.3 cm). In each forest, we exposed the bundles from April 2017 to January 2018. Due to vandalism, seven bundles could not be retrieved, resulting in a total of 143 bundles with 429 beech and 429 oak branches.

### 2.3 | Extraction of saproxylic fauna

After an 8-month exposure, we placed each bundle into a plastic tube (PVC; diameter 20 cm, length 100 cm) that acted as an emergence trap (Figure S2). The lids of the emergence traps had a hole (51 mm) covered with a fine mesh (0.5 mm) for ventilation (Figure S3). We placed the emergence traps in frames in an open shelter

situated in a forest. Thus, the emergence traps were reared under natural daily temperature fluctuations (Figure S3). To avoid differences in the rearing conditions, we randomly changed the positions of the emergence traps in the frames every month. To examine whether the rearing conditions were similar in the emergence traps, we measured the temperature inside several traps using thermo buttons (Thermo button 21 G; software ThermoTrack PC Pro 17). We obtained the emerging saproxylic organisms from attached transparent collection containers filled with 70% ethanol monthly (except January) from February to end of October 2018 (Figure S3). The taxonomic resolution applied in various insect groups and the literature used for species determination are listed in Appendix S1, and a graphical representation of the saproxylic insects extracted is depicted in Figure 1.

## 2.4 | Branch characteristics and fungal diversity (OTUs)

Macagno et al. (2015) showed that the size of a bundle can influence the colonization rate of saproxylic species. We therefore determined the volume of each bundle by measuring the diameter and length of the six branches. To assess fungal species diversity, we used subsamples of drilling chips from each branch. We used an electric drill with a bit diameter of 14 mm to obtain three drilling chip samples of each branch (at 1/4, 1/2 and 3/4 of its length) in December 2018. Within each bundle, we pooled the nine subsamples of the three beech and those of the three oak branches resulting in a total of 143 beech and 143 oak samples. The samples were weighed, freeze-dried, and milled, and the resulting fine sawdust was used for the subsequent analyses. Wood moisture

content was measured as loss during freeze-drying, and the pH was assessed in distilled water (1:10). Lignin concentration was assessed with protein-free sawdust using the acetyl bromide method (Moreira-Vilar et al., 2014).

We extracted DNA from 200 mg of each sawdust sample using the Quick-DNA Fecal/Soil Microbe Miniprep Kit (Zymo Research) following the manufacturer's instructions. DNA quantity and quality were measured using Nanodrop. We determined fungal OTUs using the F-ARISA method with the fungal-specific primer ITS1 (Gardes & Bruns, 1993) fluorescently labeled at the 5'-end (FAM) and the unlabeled ITS4 (White et al., 1990). Polymerase chain reactions (PCR; 40  $\mu$ l) consisted of 10  $\mu$ l of template DNA (20–25 ng/ $\mu$ l), 8  $\mu$ l Master Mix (5x FIREPOL Master Mix, Solis BioDyne), 1  $\mu$ l Primer ITS1-F (10  $\mu$ M), 1  $\mu$ l Primer ITS4 (10  $\mu$ M), and 20  $\mu$ l sterile water. Amplification was achieved in an Eppendorf Mastercycler Pro (Vaudaux-Eppendorf AG) under the following conditions: initial 5 min heat activation step at 95°C, followed by 35 amplification cycles of denaturation at 95°C for 60 s, annealing at 55°C for 60 s, and extension at 72°C for 90 s, with a final extension step at 72°C for 7 min. All Polymerase chain reactions were done in duplicate. PCR products were cleaned-up using the NucleoSpin gDNA Clean-up kit (Macherey-Nagel, Oensingen, Switzerland). Samples were prepared as GeneScan samples (1.5  $\mu$ l DNA sample (20 ng/ $\mu$ l); 1.5  $\mu$ l GeneScan 1200LIZ size standard; 17  $\mu$ l Hi-Di Formamide; Applied Biosystems, Life Technologies). Fragment analysis was conducted by MacroGen Inc. (Amsterdam, The Netherlands) by resolving the PCR products on a capillary sequencer (ABI 3730 XL DNA Analyzer). The size of the fluorescent amplified fragments was quantified using Peak Scanner software (version 1.0, Applied Biosystems, Inc.). Peaks with a size ranging from 390 to 1,000 bp were considered in the analyses (Ranjard et al., 2001),



**FIGURE 1** Graphical representation of the various ecological feeding guilds that occurred within the deadwood branches. Pictures of insects are of specimens that emerged from the branches

and according to Taggart et al. (2011), peak sizes obtained were rounded to the nearest base pair. To avoid possible background noise, only peaks with a signal above 1% of the sum of all peak areas were included in the analyses (Li et al., 2007). Peaks that differed in size by more than 2.0 bp were each considered as separate fungal OTU (Barto et al., 2011). The resulted OTUs of the pairs of the two PCR replicates were highly correlated (beech:  $r_s = .78$ ,  $n = 143$ ,  $p < .0001$ ; oak:  $r_s = .74$ ,  $n = 142$ ,  $p < .0001$ ).

## 2.5 | Forest site characteristics

The amount of deadwood present in a forest is a key factor determining the species assemblage of saproxylic beetles (Müller & Bütler, 2010). We therefore assessed the amount of naturally occurring deadwood within a radius of 12.62 m (500 m<sup>2</sup>) around each of the trees on which bundles were exposed using two standardized sampling methods. First, we applied the fixed area sampling (FAS) for coarse woody debris (CWD;  $\geq 7$  cm diameter;  $\geq 1$  m in length) following the guidelines of Tinner et al. (2009) and calculated the CWD volume using the method of Ligot et al. (2012). Second, we applied the line intercept sampling (LIS) for the fine woody debris (FWD) using a slightly modified method of Böhl and Brändli (2007). The LIS consisted of three 10-m-long transect lines per tree with a bundle, with the bundle acting as starting point. We recorded all FWD with a diameter measuring between 1.5 and 7 cm and with a length of  $\geq 1$  m that crossed the transect line. Furthermore, we assessed the decomposition stage of the naturally occurring deadwood by using the “Swiss army knife technique”, which enables distinguishing five stages of increasing decomposition (Tinner et al., 2009).

Tree species differ in their suitability as host for saproxylic arthropods (Parisi et al., 2018; Stokland et al., 2012). We therefore assessed the tree species richness, the abundance of each species and the breast height diameter of each tree in the 500 m<sup>2</sup> area around each focal tree in all 25 forest sites. The microclimate in a forest stand can also influence the saproxylic beetle composition (Müller et al., 2020; Seibold et al., 2016). We placed two temperature loggers (Thermo button 21 G) on two separate branch bundles in each forest site. Temperature was recorded hourly from late April until mid-November 2017. For each forest site, we used the median of the hourly recorded temperature values of the two temperature loggers in the analyses.

## 2.6 | Statistical analyses

We analyzed the data at the site level using the mean of the six bundles from each forest. Previous analyses revealed that the volume of the branch bundles and the thickness of the branches had no influence on the number of different groups of saproxylic insects that emerged and on the number of fungal OTUs. We used generalized linear models (GLM) with quasi-Poisson-distributed

errors and log-link function to test the potential effects of the degree of urbanization, forest size, forest site characteristics, and branch characteristics on the number of individuals of different taxonomic groups. Previous analyses revealed overdispersion when using the GLM models with Poisson-distributed errors. Taxonomic richness of beetles, flies, and moths was analyzed separately with the same factors using GLM but with Poisson-distributed errors.

We applied GLM with quasibinomial-distributed errors and log-link function (previous analyses revealed overdispersion when a binomial error distribution was used) to examine potential effects of the degree of urbanization, forest size, forest site characteristics, and branch characteristics on the proportion of individuals belonging to different feeding guilds (mycetophagous, saprophagous, xylophagous, predatory and parasitic). We also analyzed the proportion of beetle individuals belonging to different ecological feeding guilds with the same factors using GLM with binomial-distributed errors.

Potential effects of landscape and forest characteristics on the total number of fungal OTUs on bundles and on the number of fungal OTUs on both oak and beech branches were analyzed using similar GLM models with Poisson-distributed errors.

Because forest size and percentage forest area within a radius of 500 m were both intercorrelated with the degree of urbanization, we used the residuals of the relationship between these two variables and degree of urbanization for the GLM analyses (linear models: forest size and degree of urbanization,  $t_{1,23} = -6.14$ ,  $p < .001$ ; percentage forest within 500 m and degree of urbanization,  $t_{1,23} = -4.74$ ,  $p < .001$ ). Other forest site variables (temperature, number of living tree individuals, number of living tree species, distance to nearest beech tree, distance to nearest oak tree) were also intercorrelated and thus not considered in the analyses.

Partial redundancy analysis (pRDA) was used to determine effects of the degree of urbanization, forest size, forest, and bundle characteristics on composition of total saproxylic insect individuals and taxonomic composition of beetles (80 different species/genera; see Table 1) and on the composition of fungal OTUs on bundles. For composition of total saproxylic insect individuals, we ran pRDA analysis on two taxonomic levels: first on the level of families and second on the level of species/genera. In both analyses, we omitted singletons from the data file. Both analyses revealed very similar results. Therefore, we present only the findings of the species/genera analysis for total saproxylic insect individuals. In all cases, the “species matrices” were Hellinger-transformed prior to the analysis. Model selection was conducted by forward step-wise selection from a null model containing only degree of urbanization. In each step, the variables of the full model including forest size, forest area in the surrounding of 500 m and forest characteristics (fine woody debris volume, m<sup>3</sup>/ha), and branch bundle characteristics (wood pH, lignin and moisture content) that most significantly improved the model fit were added. This process continued until no further variable improved significantly the model fit (cut-off  $p = .05$ ). The final model was checked for variance inflation to detect collinearity of the

**TABLE 1** Total number of saproxylic individuals and taxonomic units of various arthropod groups that emerged from the branch bundles

Taxonomic group	Identified to	Number of individuals		Taxonomic units	
		Total	Median (min–max)	Total	Median (min–max)
Beetles (Coleoptera)		37,591	1,501 (478–2,722)	–	–
Bark beetles (Scolytinae)	Species	17,655	639 (0–1,919)	5	3 (0–4)
Longhorn beetles (Cerambycidae)	Species	761	18 (0–110)	8	2 (0–4)
Jewel beetles (Buprestidae)	Species	1,461	36 (0–278)	4	2 (0–4)
Rove beetles (Staphylinidae)	Species	402	4 (0–157)	12	2 (0–6)
Minute brown fungus beetles (Latridiidae)	Species/Genus	335	3 (0–143)	5	1 (0–3)
Silken fungus beetles (Cryptophagidae)	Genus	11,641	468 (41–1,105)	2	2 (1–2)
Minute hooded beetles (Corylophidae)	Genus	4,535	92 (2–992)	2	1 (1–2)
Other beetles	Species/Genus	801	19 (2–228)	42	7 (2–15)
Flies (Diptera)		136,505	3,531 (1,413–18,836)	–	–
Dark-winged fungus gnats (Sciaridae)	Family	88,230	1,872 (24–15,495)	1	1 (1–1)
Gall midges (Cecidomyiidae)	Subfamily	44,474	1,547 (781–4,156)	1	1 (1–1)
Fungus gnats (Mycetophilidae)	Family	466	1 (0–122)	1	1 (0–1)
Phorid flies (Phoridae)	Genus	181	4 (0–30)	1	1 (1–1)
Fruit flies (Drosophilidae)	Genus	91	2 (0–14)	1	1 (0–1)
Frit flies (Chloropidae)	Species	187	5 (0–28)	1	1 (0–1)
Dung midges (Scatopsidae)	Species	2,787	53 (0–471)	1	1 (0–1)
Hoverflies (Syrphidae)	Species	1	0 (0–1)	1	0 (0–1)
Craneflies (Tipulidae)	Family	1	0 (0–1)	1	0 (0–1)
Root maggot flies (Anthomyiidae)	Family	28	0 (0–26)	1	0 (0–1)
Soldier flies (Stratiomyidae)	Species	1	0 (0–1)	1	0 (0–1)
Long-legged flies (Dolichopodidae)	Genus	56	0 (0–12)	1	0 (0–1)
Lauxanid flies (Lauxaniidae)	Species	2	0 (0–1)	1	0 (0–1)
Wasps (Hymenoptera)		11,268	43 (4–194)	–	–
Chalcid wasps (Chalcidoidea)	Superfamily	5,148	157 (49–898)	1	1 (1–1)
Braconid wasps (Braconidae)	Family	5,675	191 (1–602)	1	1 (1–1)
Ichneumonid wasps (Ichneumonidae)	Family	431	11 (0–107)	1	1 (0–1)
Wood wasps (Xiphydriidae)	Family	14	0 (0–2)	1	0 (0–1)
Moths (Lepidoptera)		1,555	43 (4–194)	–	–
<i>Oecophora bractella</i> (Oecophoridae)	Species	30	0 (0–12)	1	0 (0–1)
<i>Metalampra italica</i> (Oecophoridae)	Species	1,299	33 (1–178)	1	1 (1–1)
<i>Shiffermuelleria schaefferella</i> (Oecophoridae)	Species	2	0 (0–1)	1	0 (0–1)
<i>Epicallima formosella</i> (Oecophoridae)	Species	23	0 (0–5)	1	0 (0–1)
<i>Nemapogon</i> spp. (Tineidae)	Genus	201	8 (0–18)	1	1 (0–1)
True bugs (Heteroptera)		216	5 (0–49)	–	–
<i>Xylocoris cursitans</i> (Anthocoridae)	Species	215	5 (0–49)	1	1 (0–1)
<i>Aneurus laevis</i> (Aradidae)	Species	1	0 (0–1)	1	0 (0–1)
Thrips (Thysanoptera)		72	1 (0–16)	–	–
<i>Xylaplothrips fulginosus</i>	Species	4	0 (0–1)	1	1 (0–2)
<i>Hoplothrips cortices</i>	Species	23	0 (0–16)	1	0 (0–1)
<i>Poecilothrips albopictus</i>	Species	44	0 (0–11)	1	0 (0–1)
<i>Aeolothrips versicolor</i>	Species	1	0 (0–1)	1	0 (0–1)
Barklice (Psocoptera)	Order	6,324	47 (12–2,865)	–	–

(Continues)

TABLE 1 (Continued)

Taxonomic group	Identified to	Number of individuals		Taxonomic units	
		Total	Median (min-max)	Total	Median (min-max)
Lacewings (Neuroptera) larvae	Order	2	0 (0-1)	—	—
Snakeflies (Raphidioptera)	Order	1	0 (0-1)	—	—
Total saproxylic individuals		193,534	5,740 (2,773-20,578)	—	

Note: Median (minimum and maximum) values are shown for the 25 forest sites.

variables included. Significant effects of the variables selected for the final model were tested using a post hoc ANOVA with 999 permutations. All pRDA analyses were conducted in R using the vegan package (Oksanen et al., 2017).

We used Co-inertia Analysis (COIA; Dolédec & Chessel, 1994) to assess the potential association between fungal OTUs and saproxylic beetles. Co-inertia analysis detects a common space into which the fungal OTUs and saproxylic insects can be projected and compared (Dolédec & Chessel, 1994). We first removed fungal OTUs and taxonomic units that were detected at only a single site to down weight the effects of rare species. Prior to COIA, principal component analysis (PCA) was performed on Hellinger-transformed fungal OTUs and saproxylic insects community datasets. The strength of the coupling between each paired table was evaluated with the RV coefficient. This coefficient gives a measure of overall similarity of the two datasets and takes a value between 0 and 1: the closer the coefficient approaches to 1, the stronger the correlation between the two datasets. We then used Monte-Carlo tests (with 999 random permutations) to assess the significance of the correlations. Co-inertia analysis and Monte-Carlo tests were performed with the “ade4” R package using the functions “coinertia” and “randtest”, respectively. Finally, we calculated the lengths of the arrows (Figure 7). We applied GLM models with Gaussian distribution and log-linkage to test whether the degree of urbanization, forest size, and forest and bundle characteristics affect the fungal OTU-insect association (length of the arrows). All statistical analyses were carried out using the software R (R Core Team, 2015, version R 3.3.3 and version R 3.6.1).

### 3 | RESULTS

#### 3.1 | Number of individuals and taxonomic richness of saproxylic insects

In total, 193,534 saproxylic insect individuals emerged from the branch bundles exposed in the 25 forest sites (Table 1). Beetles (Coleoptera) and flies (Diptera) were the two most abundant groups with 37,591 individuals (80 species/genera) and 136,505 individuals (13 different saproxylic fly families), respectively (Table 1). Among wasps (Hymenoptera), 11,268 individuals belonging to 4 families/superfamily emerged. Also, 1,555 individuals of saproxylic moths

emerged (5 species/genera; Table 1). Other taxonomic groups (true bugs, thrips, snakeflies, and lacewings) were represented by just a few individuals (Table 1).

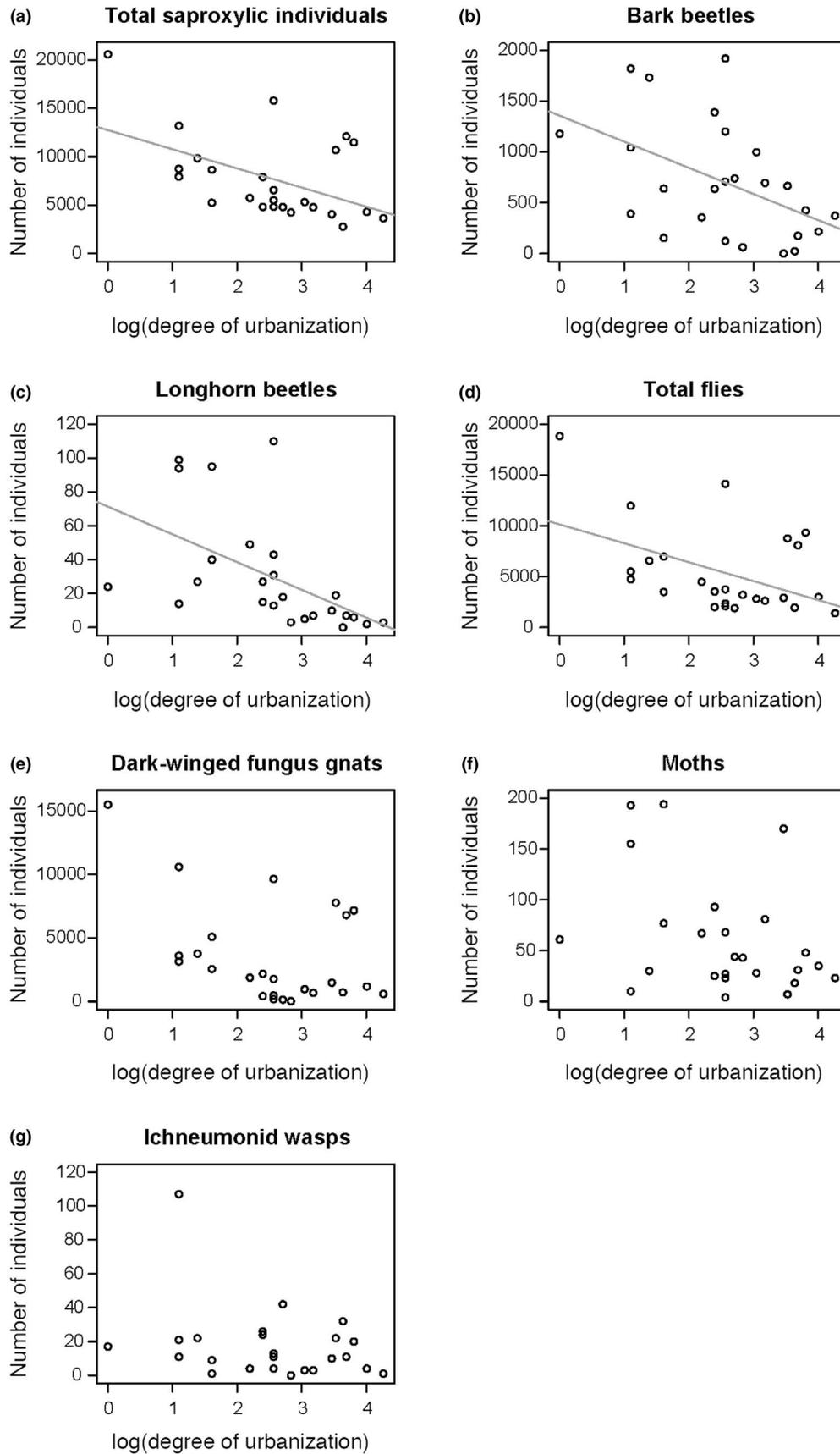
#### 3.2 | Factors influencing the number of saproxylic individuals

The 25 forest sites varied considerably in total number of saproxylic individuals that emerged from the six branch bundles (Table 1). Considering various taxonomic groups, the among-site variation in number of saproxylic individuals was most pronounced in moths (49-fold), followed by total flies (13-fold), total wasps (12-fold), and then beetles (sixfold; Table 1).

The total number of saproxylic individuals decreased with increasing degree of urbanization ( $F_{1,23} = 8.85$ ,  $p = .007$ ;  $r_s = -.48$ ,  $n = 25$ ,  $p = .016$ ; Table S2; Figure 2a). Similarly, in several insect groups the number of individuals decreased with increasing degree of urbanization: in bark beetles ( $F_{1,23} = 7.20$ ,  $p = .016$ ;  $r_s = -.47$ ,  $n = 25$ ,  $p = .019$ ; Table S2; Figure 2b), longhorn beetles ( $F_{1,23} = 16.70$ ,  $p < .001$ ;  $r_s = -.73$ ,  $n = 25$ ,  $p < .001$ ; Table S2; Figure 2c), and total flies ( $F_{1,23} = 11.82$ ,  $p = .003$ ;  $r_s = -.40$ ,  $n = 25$ ,  $p = .050$ ; Table S2; Figure 2d). Dark-winged fungus gnats were also affected by the degree of urbanization ( $F_{1,23} = 8.53$ ,  $p = .009$ ; Figure 1e), as were saproxylic moths ( $F_{1,23} = 4.89$ ,  $p = .041$ ; Table S2; Figure 2f) and ichneumonid wasps ( $F_{1,23} = 4.60$ ,  $p = .047$ ; Table S2; Figure 2g).

The numbers of jewel beetles ( $F_{1,22} = 8.07$ ,  $p = .010$ ) and chalcid wasps ( $F_{1,22} = 19.66$ ,  $p < .001$ ) were affected by forest size. Furthermore, several landscape and forest site characteristics influenced the number of saproxylic insects. The number of total flies ( $F_{1,21} = 4.57$ ,  $p = .047$ ; Table S2) was related to the percentage of forest within a radius of 500 m, while the number of dark-winged fungus gnats ( $F_{1,21} = 4.30$ ,  $p = .052$ ;  $r_s = .43$ ,  $n = 25$ ,  $p = .034$ ; Table S2) was positively influenced by the percentage of forest within a radius of 500 m.

The numbers of longhorn beetles ( $F_{1,21} = 12.77$ ,  $p = .002$ ) and gall midges ( $F_{1,21} = 4.36$ ,  $p = .050$ ; Table S2) were affected by the volume of fine woody debris (Table S2). The number of total saproxylic beetles ( $F_{1,21} = 12.44$ ,  $p = .002$ ;  $r_s = -.52$ ,  $n = 25$ ,  $p = .008$ ; Table S2) was negatively affected by a more advanced stage of decomposition of the naturally occurring deadwood. The decomposition stage also influenced the numbers of jewel beetles



**FIGURE 2** Effect of degree of urbanization on the number of (a) total saproxylic individuals, (b) bark beetles, (c) longhorn beetles, (d) total flies, (e) dark-winged fungus gnats, (f) moths, and (g) ichneumonid wasps. Lines indicate a significant correlation between the degree of urbanization and the number of individuals of the different insect groups

**TABLE 2** Number of individuals and taxonomic units belonging to different feeding guilds that emerged from the branch bundles exposed in the 25 forest sites

Taxonomic group	Number of individuals		Taxonomic units	
	Total	Median (min–max)	Total	Median (min–max)
Total mycetophagous individuals	147,493	4,143 (1,924–18,769)	32	13 (6–16)
Beetles	12,508	489 (48–1,146)	18	6 (2–8)
Flies	133,358	3,511 (1,411–18,659)	5	4 (2–4)
Dark-winged fungus gnats (Sciaridae)	88,230	1,872 (24–15,495)	1	1 (1–1)
Gall midges (Cecidomyiidae)	44,474	1,547 (781–4,156)	1	1 (1–1)
Other mycetophagous Diptera	654	8 (0–125)	3	2 (0–2)
Moths (Oecophoridae and Tineidae)	1,555	43 (4–194)	5	3 (1–4)
Bark bugs (Aradidae)	1	0 (0–1)	1	0 (0–1)
Thrips (Thysanoptera)	71	1 (0–16)	3	1 (0–2)
Total saprophagous individuals	13,785	370 (52–2,996)	–	–
Beetles	4,552	92 (3–992)	3	1 (1–3)
Flies	2,909	83 (0–472)	5	2 (0–3)
Barklice (Psocoptera)	6,324	47 (12–2,865)	1	1 (1–1)
Total xylophagous individuals	19,857	682 (25–2,115)	–	–
Beetles	19,843	681 (25–2,113)	30	8 (4–14)
Bark beetles (Scolytinae) <sup>a</sup>	17,566	636 (0–1,918)	3	2 (0–3)
Longhorn beetles (Cerambycidae)	761	18 (0–110)	8	2 (0–4)
Jewel beetles (Buprestidae)	1,461	36 (0–278)	4	2 (0–4)
Snout beetles (Curculionidae)	27	1 (0–7)	6	1 (0–2)
Other beetles	28	1 (0–4)	9	1 (0–3)
Wood wasps (Xiphydriidae)	14	0 (0–2)	1	0 (0–1)
Total predatory individuals	964	30 (4–180)	–	–
Beetles	688	17 (1–172)	29	6 (1–12)
Flies	57	1 (0–12)	2	1 (0–1)
Minute pirate bugs (Anthocoridae)	215	5 (0–49)	1	1 (0–1)
<i>Aeolothrips versicolor</i> (Thysanoptera)	1	0 (0–1)	1	0 (0–1)
Neuroptera larvae	2	0 (0–1)	1	0 (0–1)
Raphidioptera	1	0 (0–1)	1	0 (0–1)
Total parasitic wasps	11,254	454 (98–1,210)	–	–
Chalcid wasps (Chalcidoidea)	5,148	157 (49–898)	1	1 (1–1)
Braconid wasps (Braconidae)	5,675	191 (1–602)	1	1 (1–1)
Ichneumonid wasps (Ichneumonidae)	431	11 (0–107)	1	1 (0–1)

Note: Median (minimum and maximum) values of the forest sites are shown.

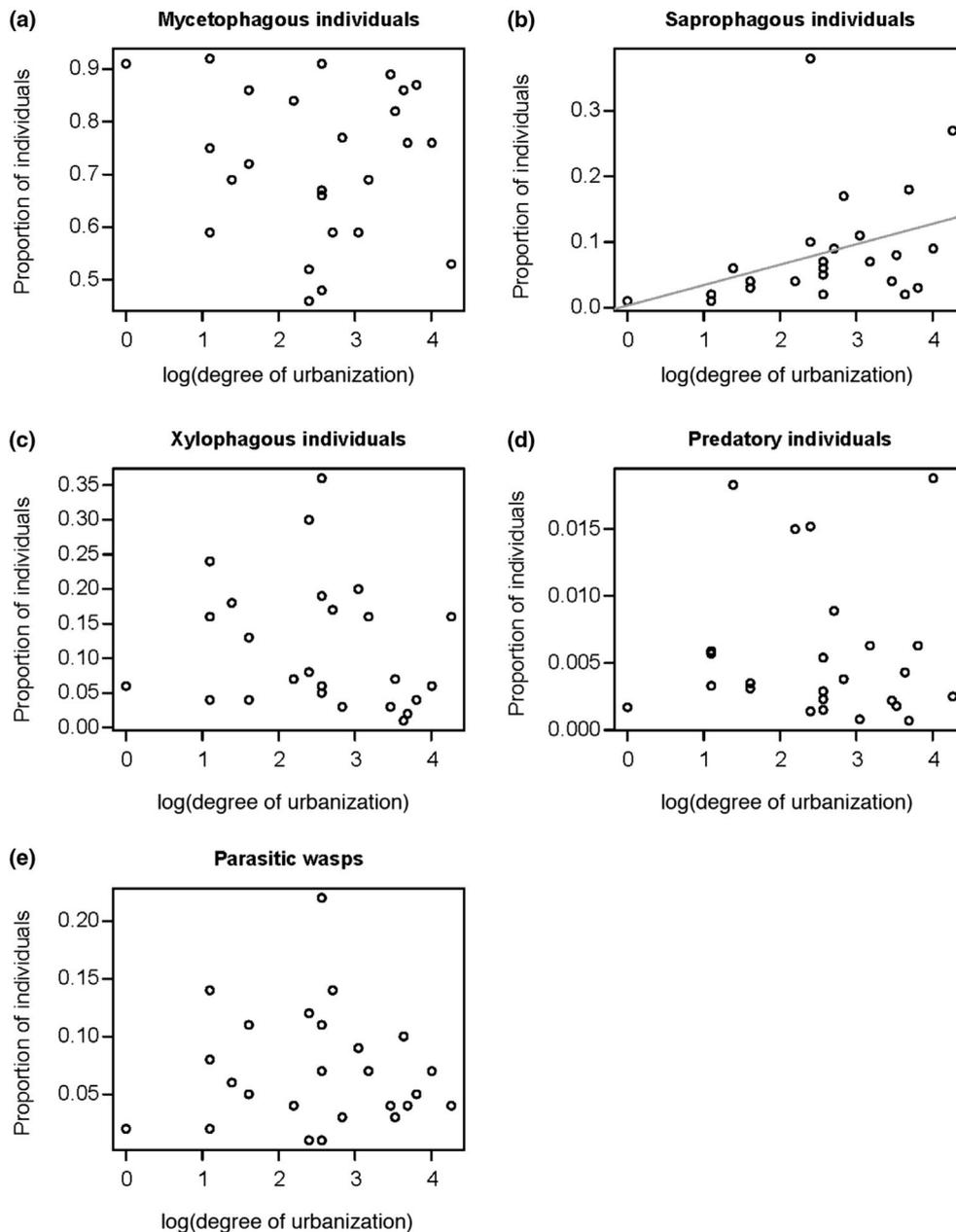
<sup>a</sup>Excluding *Ambrosia* bark beetles which were categorized within the mycetophagous beetles.

( $F_{1,21} = 4.64$ ,  $p = .044$ ; Table S2) and chalcid wasps ( $F_{1,20} = 18.93$ ,  $p = .003$ ; Table S2). The numbers of total flies ( $F_{1,18} = 4.88$ ,  $p = .041$ ;  $r_s = .53$ ,  $n = 25$ ,  $p = .005$ ; Table S2), dark-winged fungus gnats ( $F_{1,19} = 4.82$ ,  $p = .042$ ;  $r_s = .62$ ,  $n = 25$ ,  $p = .001$ ; Table S2), other flies (other than the dominant fly families, dark-winged fungus gnats and gall midges;  $F_{1,18} = 14.54$ ,  $p = .001$ ;  $r_s = .63$ ,  $n = 25$ ,  $p < .001$ ; Table S2), and saproxylic moths ( $F_{1,17} = 4.54$ ,  $p = .048$ ;  $r_s = .51$ ,  $n = 25$ ,  $p = .010$ ; Table S2) all increased with increasing wood moisture content of branches. The number of longhorn

beetles was affected by wood pH of the branches ( $F_{1,18} = 4.48$ ,  $p = .049$ ; Table S2).

### 3.3 | Taxonomic richness of saproxylic insects

Taxonomic richness of beetles, flies, and moths was not significantly influenced by the degree of urbanization, forest size, or any other forest site or branch characteristics (Table S3).



**FIGURE 3** Effect of degree of urbanization on the proportion of (a) total mycetophagous, (b) saprophagous, (c) xylophagous, (d) predatory, and (e) parasitic wasp individuals

### 3.4 | Number of individuals and taxonomic richness of ecological feeding guilds of saproxylic insects

The saproxylic individuals were assigned to five feeding guilds (mycetophagous, saprophagous, xylophagous, predatory and parasitoid; Table S4) in all taxonomic groups. In total, there were 147,493 mycetophagous individuals. Among them, we recorded 12,508 mycetophagous beetles belonging to 18 species (Table 2). We also recorded 133,358 mycetophagous fly individuals belonging to five families (Table 2).

We found 13,785 saprophagous individuals. Among them, there were 4,552 saprophagous beetle individuals comprising of

three species. Regarding saprophagous flies, there were 2,909 individuals comprising of five families (Table 2). A total of 19,857 xylophagous individuals were recorded. The majority of them were xylophagous beetles (19,843 individuals) comprising of 30 species (Table 2). We found 964 predatory individuals. Among them, there were 688 predatory beetles belonging to 29 predatory species (Table 2). There were 11,254 parasitic wasp individuals (Chalcidoidea, Braconidae, and Ichneumonidae combined) belonging to three families/superfamily (Table 2). We also found 181 individuals of Phoridae flies (genus *Megaselia*) that could not be assigned to a functional group. These individuals were added to the total saproxylic individuals (Table 2), but not further considered in the analyses.

### 3.5 | Factors influencing the proportion of individuals belonging to different feeding guilds

Among the feeding guilds, the proportion of saprophagous individuals increased with increasing degree of urbanization ( $F_{1,23} = 24.48$ ,  $p < .001$ ;  $r_s = .53$ ,  $n = 25$ ,  $p = .006$ ; Table S5; Figure 3b). In contrast, the proportion of saprophagous individuals decreased with increasing forest size ( $F_{1,22} = 18.47$ ,  $p < .001$ ;  $r_s = -.40$ ,  $n = 25$ ,  $p = .046$ ; Table S5) and was affected by the percentage of forest within a radius of 500 m ( $F_{1,21} = 8.25$ ,  $p = .011$ ; Table S5). Furthermore, the proportion of saprophagous individuals was negatively related to the stage of decomposition of the naturally occurring deadwood ( $F_{1,19} = 10.81$ ,  $p = .004$ ;  $r_s = -.44$ ,  $n = 25$ ,  $p = .029$ ; Table S5) and decreased with increasing wood moisture content ( $F_{1,17} = 9.35$ ,  $p = .007$ ;  $r_s = -.68$ ,  $n = 25$ ,  $p < .001$ ; Table S5). In contrast, the proportions of individuals belonging to the other feeding guilds (mycetophagous, xylophagous, predatory, and parasitoid) were neither influenced by the degree of urbanization nor by the size of the forests (Table S5; Figure 3). However, the proportion of mycetophagous individuals was affected by the percentage of forest within a radius of 500 m ( $F_{1,21} = 6.12$ ,  $p = .025$ ; Table S5) and was positively related to the stage of decomposition of naturally occurring deadwood ( $F_{1,18} = 16.99$ ,  $p < .001$ ;  $r_s = .48$ ,  $n = 25$ ,  $p = .015$ ; Table S5). Furthermore, the proportion of mycetophagous individuals increased with increasing wood moisture content of the branches ( $F_{1,17} = 12.52$ ,  $p = .003$ ;  $r_s = .69$ ,  $n = 25$ ,  $p < .001$ ; Table S5). Considering parasitic wasps, their proportion was only affected by the decomposition stages of naturally occurring deadwood ( $F_{1,20} = 6.36$ ,  $p = .020$ ; Table S5).

### 3.6 | Proportion of taxonomic richness of ecological feeding guilds

The proportion of taxonomic richness of total mycetophagous, saprophagous, xylophagous, and predatory individuals and the taxonomic richness of mycetophagous, saprophagous, xylophagous, and predatory beetles were not significantly influenced by either the degree of urbanization, forest size, or any other forest site or branch characteristics (Table S6).

### 3.7 | Total insect taxonomic composition and composition of beetles

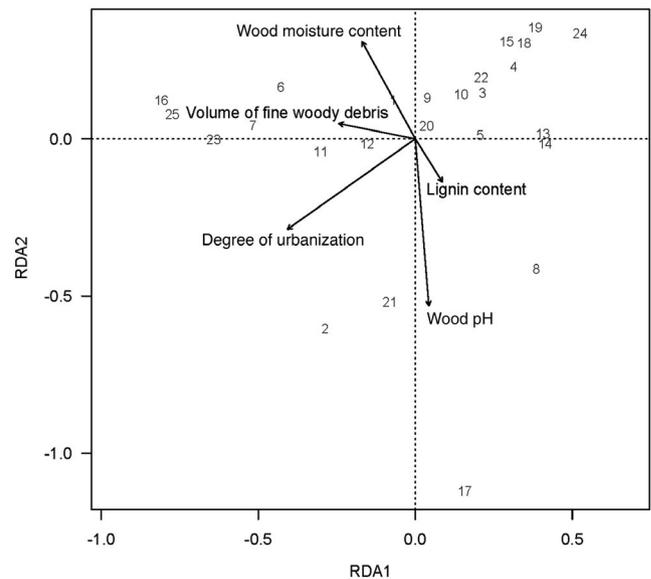
Partial redundancy analyses revealed that the composition of total saproxylous insect individuals was neither altered by the degree of urbanization nor by forest size. The permutation analysis for the pRDA analysis showed that the wood moisture content of the branches ( $F_{1,19} = 6.00$ ,  $p = .001$ ) significantly changed the composition of total saproxylous insect individuals. Furthermore, the percentage of forest area within 500 m tended to affect the composition of total saproxylous insect individuals ( $F_{1,19} = 2.29$ ,  $p = .053$ ).

Considering saproxylous beetles, both the degree of urbanization ( $F_{1,19} = 5.92$ ,  $p = .001$ ) and the wood pH of the branches ( $F_{1,19} = 2.66$ ,  $p = .025$ ) altered the taxonomic composition of the beetles (Figure 4). Furthermore, the volume of fine woody debris ( $F_{1,19} = 2.11$ ,  $p = .063$ ) and the lignin content of the branches ( $F_{1,19} = 2.10$ ,  $p = .070$ ) tended to change the taxonomic composition of the beetles (Figure 4). The permutation test further revealed that these factors significantly separated the taxonomic composition of the beetles along the first ( $F_{1,19} = 6.39$ ,  $p = .003$ ) and second axis ( $F_{1,19} = 5.64$ ,  $p = .003$ ; Figure 4).

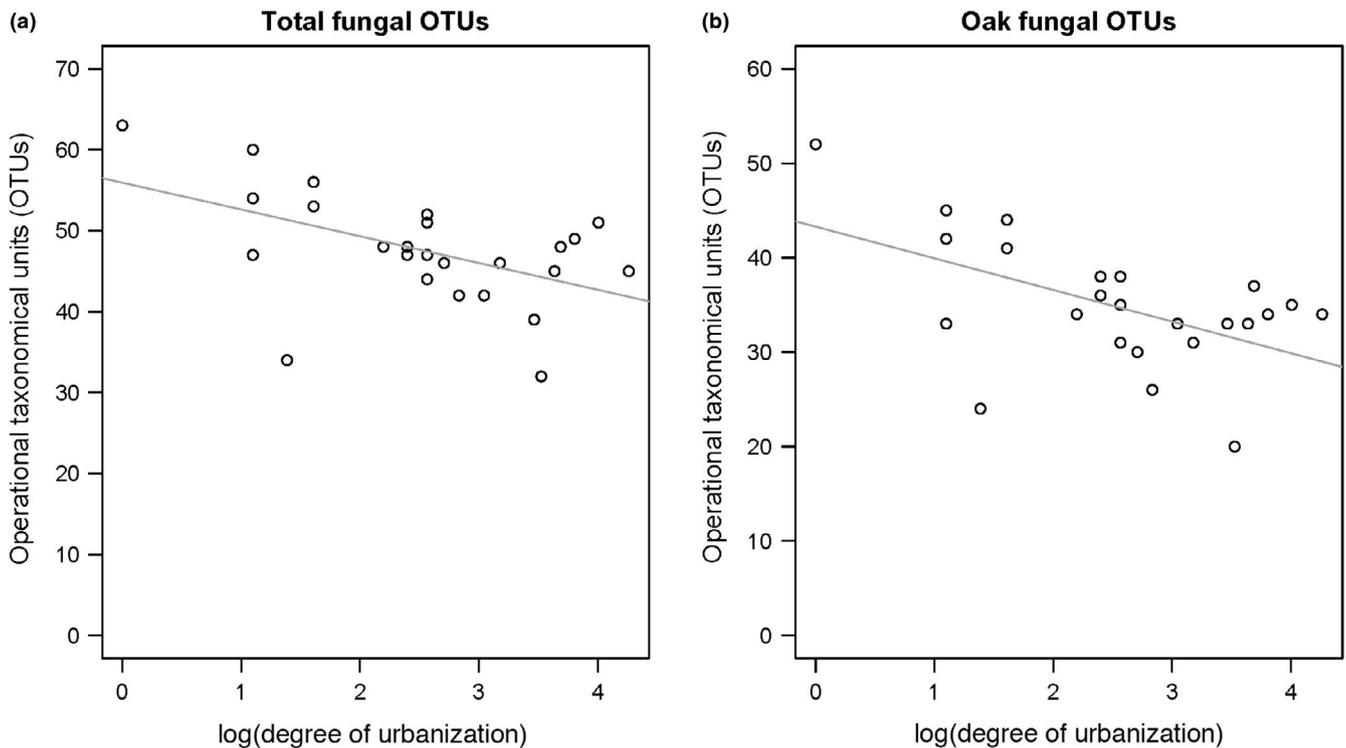
### 3.8 | Diversity and composition of fungal species (OTUs)

Out of a total of 97 fungal OTUs that were recorded in the branch bundles exposed in the 25 forest sites, 90 fungal OTUs were found on beech branches and 91 fungal OTUs on oak branches. Total number of fungal OTUs ranged from 32 to 63 across the forest sites (median: 47 OTUs). The corresponding figures for the number of fungal OTUs found on beech branches were 26–44 (34) and 20–52 (34) for oak branches.

Total number fungal OTUs found on the entire bundles decreased with increasing degree of urbanization ( $\chi^2_{1,23} = 6.31$ ,  $p = .012$ ;  $r_s = -.46$ ,  $n = 25$ ,  $p = .020$ ). Similarly, the number of fungal OTUs found exclusively on oak branches decreased with increasing degree of urbanization ( $\chi^2_{1,23} = 8.84$ ,  $p = .003$ ;  $r_s = -.41$ ,  $n = 25$ ,  $p = .042$ , Table S7; Figure 5a, b). In contrast, the number of fungal OTUs on beech branches was not affected by the degree of urbanization (Table S7).



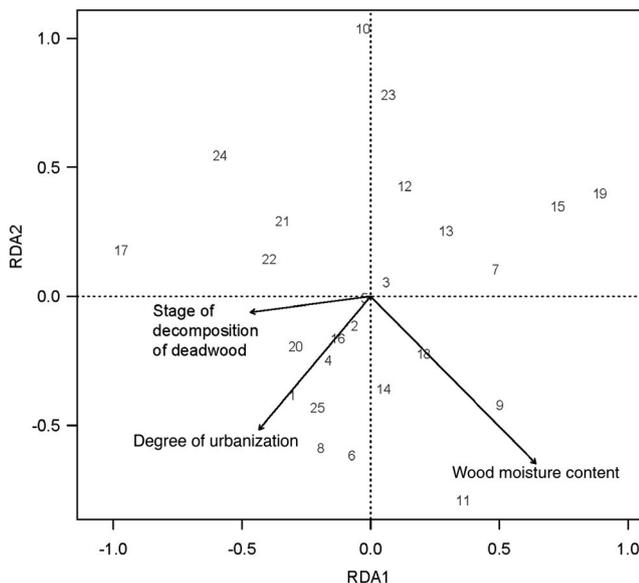
**FIGURE 4** Results of constrained ordination analysis (RDA) showing the relationship of the taxonomic composition of beetles that emerged from the branch bundles exposed in 25 forests to the degree of urbanization and forest characteristics such as volume of fine woody debris and branch bundle characteristics including wood pH, wood moisture and lignin content (only significant variables are shown)



**FIGURE 5** Effect of degree of urbanization on (a) the total number of fungal OTUs found on the branch bundles and (b) the number of fungal OTUs only found on oak branches

Overall, the size of the forests did not influence the number of total fungal OTUs as well as the number of fungal OTUs on beech and oak branches (all  $p > .20$ ; Table S7). Considering forest site characteristics,

both the total number of fungal OTUs and those found exclusively on oak branches were positively influenced by the volume of fine woody debris (total:  $\chi^2_{1,20} = 4.21$ ,  $p = .040$ ;  $r_s = .45$ ,  $n = 25$ ,  $p = .025$ ; oak:  $\chi^2_{1,20} = 4.91$ ,  $p = .027$ ;  $r_s = .45$ ,  $n = 25$ ,  $p = .023$ ; Table S7).



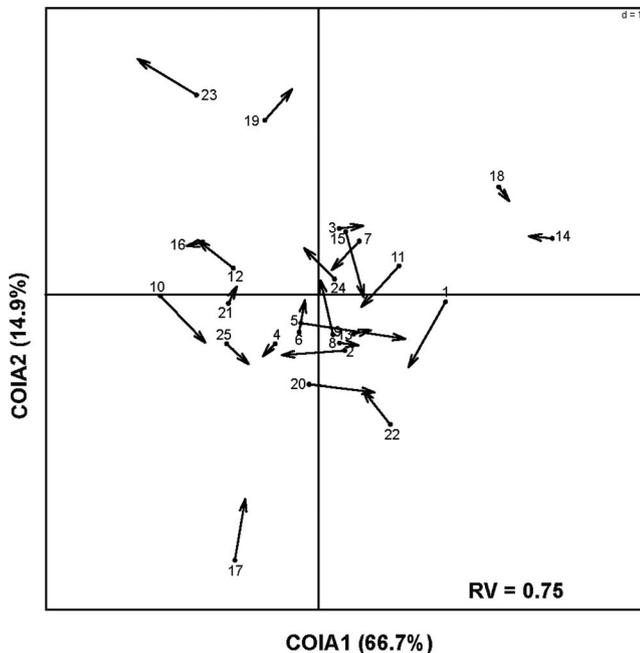
**FIGURE 6** Results of constrained ordination analysis (RDA) showing the relationship of the taxonomic composition of fungal OTUs detected on branch bundles exposed in 25 forests to the degree of urbanization, stage of decomposition of naturally occurring deadwood in the forest sites and wood moisture content of the branch bundles exposed (only significant variables are shown)

Partial RDA showed that the degree of urbanization altered the composition of total fungal OTUs (Permutation test:  $F_{1,21} = 1.46$ ,  $p = .048$ ; Figure 6). Furthermore, decomposition stage of the naturally occurring deadwood ( $F_{1,21} = 1.45$ ,  $p = .050$ ) and the wood moisture content of the branches ( $F_{1,21} = 1.42$ ,  $p = .072$ ) affected the composition of total fungal OTUs. Considering the fungal OTUs found on beech branches, their composition was affected by the wood pH of the beech branches ( $F_{1,23} = 2.19$ ,  $p = .033$ ). Wood pH also separated fungal OTU composition on beech branches along the first RDA axis ( $F_{1,23} = 2.19$ ,  $p = .027$ ). In contrast, fungal OTU composition on oak branches was influenced both by the degree of urbanization ( $F_{1,22} = 2.14$ ,  $p = .029$ ) and wood pH of branches ( $F_{1,22} = 2.25$ ,  $p = .014$ ). Furthermore, the degree of urbanization separated the composition of the fungal OTUs along the first RDA axis ( $F_{1,22} = 2.99$ ,  $p = .014$ ).

The compositions of fungal OTUs found on either beech or oak branches were not associated ( $RV = 0.29$ ,  $p = .465$ ).

### 3.9 | Association between total fungal OTUs and total saproxylic insects

Co-inertia analysis revealed a significant association between the composition of total fungal OTUs and that of the total saproxylic



**FIGURE 7** Co-inertia analysis (COIA) between the compositions of total fungal OTUs and the total saproxylic insect individuals. The arrows link the co-inertia scores resulting from the fungal OTUs data set to that obtained from the saproxylic insect data set. Circles locate sites as ordinated by fungal OTU composition, whereas arrows indicate the ordination of saproxylic insects

insect individuals ( $RV = 0.75$ ,  $p = .005$ ; Figure 7). The first two axes accounted for 80.4% of the total variance in fungi–saproxylic insects comparison (Figure 7).

The lengths of the arrows shown in Figure 7 illustrate the concordance between the two datasets. The shorter the arrows, the better the concordance between the composition of fungal OTUs and that of total saproxylic insects. Generalized linear model analysis revealed that the lengths of the arrows were exclusively related to the degree of urbanization ( $F_{1,23} = 4.98$ ,  $p = .036$ ), indicating that the association between OTU composition of fungi and that of saproxylic insects altered along the rural–urban gradient.

## 4 | DISCUSSION

### 4.1 | Effects of degree of urbanization on saproxylic individuals

Our study showed that the abundance of several groups of saproxylic insects including bark beetles, longhorn beetles, and total flies decreased in forests situated in increasingly urbanized areas, while forest size and local forest characteristics appeared to have a minor influence on the abundance of these insect groups. Furthermore, the total number of fungal OTUs (a potential proxy for fungal species richness) decreased with increasing degree of urbanization in the surroundings of the forests examined and was positively influenced by the volume of fine woody debris in the forest site. Thus, our study

provides evidence that urbanization negatively impacts saproxylic insects and fungi.

Understanding how landscape characteristics affect biodiversity patterns at local and landscape scales is important for promoting biodiversity in urban environments (Beninde et al., 2015). In our study, the abundance of total saproxylic individuals was negatively related to the degree of urbanization. This finding is in line with the results of a recent study conducted in Belgian cities (Piano et al., 2020) and a global meta-analysis showing that terrestrial arthropods were less abundant and diverse in more urbanized landscapes (Fenoglio et al., 2020). In contrast to these studies, we did not record any effect of degree of urbanization on the composition of total saproxylic insect individuals.

In our study, flies were the most abundant taxonomic group comprising of 71% of all saproxylic individuals. The observed negative effect of urbanization on total number of saproxylic individuals mainly resulted from a reduced number of flies recorded in forests situated in highly urbanized areas (Figure 2). Similar decreases in the abundance and/or richness of several fly families in urban areas were reported in other studies (total flies: Theodorou et al., 2020; Drosophilidae flies: Gottschalk et al., 2007; Chloropidae: Kozlov & Zvereva, 1997 and phorid flies: Durska, 1981). However, a high habitat quality (abundance of floral resources) in urban areas can support a high fly richness (Theodorou et al., 2020). Regarding saproxylic flies, no study assessed so far the effect of urbanization on this insect group.

Considering saproxylic moths, the number of individuals declined with increasing degree of urbanization, similar to the pattern found in the meta-analysis of Fenoglio et al. (2020). Piano et al. (2020) also demonstrated that with increasing degree of urbanization macro-moths became less diverse. Furthermore, several saproxylic moths had lower abundances in forest fragments than in large continuous old-growth forests (Komonen et al., 2000). In urban environments, light pollution may disrupt movement of nocturnal moths between habitat patches and contribute to their decline (Bates et al., 2014). However, a study in Basel found that moths in urban areas exposed to strong light pollution (near streetlights) have a reduced flight-to-light behavior compared to those in rural populations (Altermatt & Ebert, 2016). The altered flight-to-light behavior may allow moth populations to persist in an urban setting.

Parasitoids (including the three wasp families/superfamilies recorded in our study) are an integral part of the saproxylic food web (Hilszczański, 2018). Many parasitoids are characterized by low abundances (Fenoglio & Salvo, 2010). It has therefore been suggested that parasitoids are more negatively affected by habitat fragmentation than their hosts (Tscharntke & Brandl, 2004). This has partly been confirmed as some parasitoids, including ichneumonid wasps, were found in lower abundances, species richness, and parasitism rates with increasing degree of urbanization (Fenoglio & Salvo, 2010). Similarly, we found a lower abundance of ichneumonid wasps in isolated urban forests than in rural forests (Figure 2), which might reduce the natural enemy regulation ecosystem service they provide (Fenoglio et al., 2020; Nelson & Forbes, 2014).

As we expected, total abundance and richness of saproxylic beetles were not affected by the degree of urbanization. In terms of species richness of saproxylic beetles, the importance of deadwood becomes more prominent with increasing spatial scales (Franc et al., 2007). However, the abundance of bark beetles comprising 47% of the saproxylic beetles and that of the longhorn beetles (2%) decreased with increasing degree of urbanization (Figure 2). As pioneer saproxylics, bark beetles colonize the early decay stage of deadwood (Parisi et al., 2018). Many bark beetle species are good dispersers and can find fresh deadwood substrates several kilometers away from their starting location (Komonen & Müller, 2018), even within an urban setting (Piel et al., 2005). However, using a rural–urban gradient approach, Piel et al. (2005) showed that the spruce bark beetle (*Ips typographus*) reached the highest abundance in areas with a moderate level of urbanization and that the abundance of bark beetles in the city center was negatively influenced by building density. In our study, the reduced abundance of beech bark beetles (*Taphrorychus bicolor*) in highly urbanized forests could be the result of dispersal barriers in urban areas and the difficulty in locating viable beech and oak hosts via volatiles or aggregation pheromones (Piel et al., 2005).

We also recorded a shift in total beetle species composition along the urbanization gradient. This result parallels the findings of some studies showing that urbanization changes the species composition of nonsaproxylic carabid beetles (Niemelä & Kotze, 2009) and that of staphylinid beetles (Magura et al., 2013) and of microarthropod litter communities in urban forests (Malloch et al., 2020), and thus may reduce the functional diversity of the beetle community (Hagge et al., 2019).

## 4.2 | Effects of forest size and local forest characteristics

Forest size and local forest characteristics including the amount of deadwood, its decay stage and moisture content have the potential to influence the abundance, species richness, and composition of saproxylic insects (Hagge et al., 2019; Lassaue et al., 2011; Seibold et al., 2015). In our study, forest size did not affect the abundance and species richness of most taxonomic groups with the exception of jewel beetles and chalcid wasps. Grohmann et al. (2003) also found no effect of forest size on the abundance of saproxylic beetles. This might frequently be the case for pioneer saproxylic species as investigated in our study. Pioneer saproxylic species often prefer single trees, forest edge habitats, and forests with an open canopy (Bouget et al., 2013; Müller et al., 2015; Vodka et al., 2009). The dominant bark beetles in our study (*T. bicolor* and *S. intricatus*) occur at sunny forest edges as well as in shaded forest interiors (Kappes & Topp, 2004; Vele & Horák, 2018; Wermelinger et al., 2007), and thus, no forest size–abundance relationship can be expected.

Urban broad-leaved forests are regularly disturbed by recreational activities and frequently by intensive forest management,

which can reduce the amount of deadwood, the essential resource for deadwood-dependent organisms (Müller & Bütler, 2010; Ódor et al., 2006). In our study, only the abundances of longhorn beetles, gall midges, and ichneumonid wasps were influenced by the volume of fine woody debris, but not by the volume of coarse woody debris. The majority of studies on saproxylics investigated the role of the amount of CWD and found a positive effect on the abundance and species richness of saproxylic insects (Lassaue et al., 2011; Seibold et al., 2015; Vanderwel et al., 2006). Most saproxylics show a preference for a certain deadwood diameter range (Brin et al., 2011; Schiegg, 2001); thus, the saproxylics emerging from the branches in our study responded more to FWD than to CWD in the surroundings. Vodka et al. (2009) reported a weak relationship between FWD and the abundance of saproxylic insects. Pioneer saproxylics in fine woody debris as investigated in our study are less sensitive to disturbance or changes in specific local habitat characteristics and may therefore respond on a larger landscape scale (Franc et al., 2007; Gossner et al., 2013; Økland et al., 1996; Schiegg, 2001). Apart from ichneumonid wasps, the other parasitic wasps may have great dispersal capabilities similar to their primary saproxylic beetle hosts and are therefore not bound to local deadwood resources (Gibb et al., 2008).

The decay stage of deadwood determines the abundance and species richness of saproxylics such as beetles, flies, and parasitic wasps (Gossner et al., 2013; Vanderwel et al., 2006). In our study, we considered the early decay stages of beech and oak branches and thus early colonizers on deadwood (Vanderwel et al., 2006). We only found an effect of the decay stages on the abundance of jewel beetles and chalcid wasps. Furthermore, the quality of deadwood can influence the abundance and species richness of saproxylic insects (Lassaue et al., 2011). In accordance with other studies (Hibbert, 2010; Hövemeyer & Schauer mann, 2003; Irmeler et al., 1996), we found that moisture content of the branches affected the abundance of flies and the proportion of mycetophagous individuals. Higher moisture content of branches provides ideal microclimatic conditions for the proliferation of deadwood fungi (Bässler et al., 2010), which in turn promotes mycetophagous flies, especially the dark-winged fungus gnats with short generation length (Vanderwel et al., 2006). In addition, higher moisture content caused a significant shift in composition of total saproxylic insect individuals, probably by providing more ideal microclimatic conditions for mycetophagous beetles, flies, and moths (Thorn et al., 2018; Vanderwel et al., 2006). The shift in beetle species composition as a result of changed pH and lignin content of the dead wood branches could be caused by differences in fungal enzyme activity (Baldrian et al., 2016) and thus available decayed organic material for certain beetles to feed on.

## 4.3 | Effects of degree of urbanization and local forest characteristics on saproxylic fungi

Saproxylic fungi are key players in the breakdown of deadwood and provide food resources for saproxylic insects (Birkemoe et al., 2018). We found a negative effect of the degree of

urbanization on both the total number of OTUs and the number of fungal OTUs exclusively occurring on oak branches. The reduction in number of fungal OTUs may be caused by the fragmentation of the forests and associated changes in microclimatic conditions (lower humidity). Furthermore, the lower number of fungal OTUs in forests situated in highly urbanized areas could be a result of limited dispersal of spores in fragmented forests (Kausserud et al., 2005; Küffer & Senn-Irlet, 2005; Siitonen et al., 2005). Although fungal spores can be transported over large distances by wind and small animals (Komonen & Müller, 2018), fragmentation-reduced spore dispersal may result in a decline in the re-colonization of fungi species, especially in specialized fungi (Lonsdale et al., 2008). The microclimatic conditions in a forest affect fungal growth and fruiting, particularly in fungi growing on fine woody debris (Bässler et al., 2010). This might partly explain the lower fungal richness in forests in urban areas with a high temperature. In contrast to another study, we found no effect of forest size on the number of fungal OTUs (Küffer & Senn-Irlet, 2005).

The positive impact of increasing volume of fine woody debris on total OTUs and fungal OTUs on oak branches indicates that the kind of forest management is important for promoting saproxylic fungi. We observed piles of branches left after logging in the forests. In the short to mid-term (5–10 years), the amount of fine woody debris can increase the number of common fungi species (Pasanen et al., 2014) and might be important for the preservation of rare fungal species in intensively managed forests (Küffer & Senn-Irlet, 2005; Nordén et al., 2004).

The degree of urbanization also caused shifts in the composition of fungal OTUs. Additionally, as reported in previous studies (Hoppe et al., 2016), physical–chemical properties of branches (wood pH and moisture) influenced the species composition of saproxylic fungi.

#### 4.4 | Effect of degree of urbanization on the proportion of mycetophagous and saprophagous insects

Surprisingly, the proportion of mycetophagous individuals was neither affected by the degree of urbanization nor by forest size. A previous study found a lower number of forest-dwelling (mainly saprophilous and mycetophilous) staphylinid species in urban areas, probably because of increased dryness and reduction in organic matter on the forest floor (Magura et al., 2013). The fact that we actually found a higher proportion of saprophagous individuals in urban areas might be a result of the dominance of the cosmopolitan beetle *Sericoderus lateralis* (Corylophidae) that can reproduce asexually and thrives in cities around the world (Bowstead, 1999).

#### 4.5 | Insect–fungi association

In pieces of deadwood, fungi breakdown lignin and cellulose and detoxify secondary chemicals such as phenols, thus allowing access

for saproxylic insects (Biedermann & Vega, 2020). Previous studies found that saprophagous and mycetophagous insects were associated with saproxylic fungi and that species richness of saproxylic insects increased with increasing fungal richness (Floren et al., 2015; Persiani et al., 2010). In accordance with these studies, we found significant associations between fungal OTUs and saproxylic insects. Urbanization negatively affected some saproxylic groups, which may disturb the saproxylic community network. In our study, the altered species composition of fungal OTUs with increasing degree of urbanization might have changed the interactions between saproxylic insect species and fungal OTUs.

## 5 | CONCLUSIONS

Our study showed that alterations in abundances of saproxylic insects and the number of fungal OTUs along a rural–urban gradient could be driven by urbanization, and also partly by local characteristics (e.g., deadwood amount) and branch characteristics (wood moisture). This ultimately led to changes in taxonomic composition and altered linkages between saproxylic insect and fungi in urban areas, which in turn may influence the ecosystem functions of wood decomposition and nutrient recycling in urban forests.

Forest management could promote saproxylic insect and fungal diversity by increasing the amount of deadwood of various diameters including FWD in urban forests. Urban forests play an essential role for recreational activities. For security reasons this fact has to be taken into account when promoting standing deadwood (Fröhlich & Ciach, 2020). An alternative measure but not a real substitute for standing deadwood and large deadwood logs could be assembling and providing piles of branches that may serve as a refuge for some saproxylic insects (Jonsell et al., 2007) and fungi (Pasanen et al., 2014).

## ACKNOWLEDGMENTS

We would like to thank the forest owners and foresters in charge for allowing us access to the forests. Adrian Amsler and Markus Lack (foresters at Bürgergemeinde Allschwil) prepared the beech and oak branches and made the shelter available for the emergence traps. We also thank Hans Meyer for help in construction of the wooden frames for the emergence traps. We thank Benedikt Feldmann for identification of staphylinid beetles, Manfred Ullitzka for identifying the Thysanoptera and Christoph Germann and Paul Beuk for verifying weevils and Diptera identifications. Brigitte Braschler, Ryan Garrick, and two anonymous reviewers commented on an earlier version of the manuscript. Financial support was received from the Emilia Guggenheim-Schnurr Stiftung, the Basler Stiftung für Biologische Forschung, and the Basler Stiftung für experimentelle Zoologie.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTION

**Sandro Meyer:** Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Hans-Peter Rusterholz:** Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (equal); Writing-review & editing (supporting). **Bruno Baur:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (lead); Software (lead); Supervision (equal); Validation (lead); Writing-review & editing (equal).

## DATA AVAILABILITY STATEMENT

The abundance data of the saproxylic insects, the number of fungal OTUs, the taxonomic richness, and proportion of insects belonging to different feeding guilds, as well as the local forest site and landscape characteristics and branch characteristics, are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.gf1vhhmn>).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Meyer S, Rusterholz H-P, Baur B. Saproxylic insects and fungi in deciduous forests along a rural-urban gradient. *Ecol Evol*. 2021;11:1634–1652. <https://doi.org/10.1002/ece3.7152>

## Supplementary material Chapter III

**Appendix S1** Taxonomical resolution and literature used for species determination

**Table S1** Characteristics of forest sites

**Table S2** GLM analyses examining the effects of the degree of urbanisation, forest size, local characteristic and branch characteristics on the total number of individuals and various saproxylic insect groups

**Table S3** GLM analyses of the beetle, flies, and moth taxonomic richness

**Table S4** Classification of saproxylic individuals into feeding guilds

**Table S5** GLM analyses examining the effects of the degree of urbanisation, forest size, local characteristic and branch characteristics on the proportion of insect individuals belonging to different feeding guilds

**Table S6** GLM analyses examining the effects of the degree of urbanisation, forest size, local characteristic and branch characteristics on the proportion of total and beetle mycetophagous, saprophagous, xylophagous, and predatory taxonomic richness

**Table S7** GLM analyses examining the effects of the degree of urbanisation, forest size, local characteristic and branch characteristics on the number of total fungal species (OTUs) on the branches exposed and separately the number of fungal species on both the beech and oak branches exposed in the 25 forests

**Figure S1** Map of 25 forests sites

**Figure S2** Example of a branch bundle attached to a tree stem

**Figure S3** Emergence traps set up

## **Appendix S1. Taxonomical resolution and literature used for species determination.**

The collected bark beetles (Scolytinae) were identified to species level using the key of Grüne (1979). Staphylinidae were identified to species level (apart from one individual of the sub-family Pselaphinae) by Benedikt Feldmann using the keys of (Freude et al., 1974; Lohse, 1989; Assing, 1999; 1998; Assing & Schülke 2001; 2007; 2012; Schülke & Smetana, 2015). Other beetles (including saproxylic beetles) were identified when possible to species level using the key of Lompe (2010). The bark lice (Psocoptera), snakeflies (Raphidioptera) and net-winged insects (Neuroptera) were determined to the order level and true bugs (Heteroptera) and flies (Diptera) to the family level using Stresemann (2011), Unwin (1984) and Oosterbroek (2006). Among the Hymenoptera, the chalcid wasps (Chalcidoidea) were determined to the superfamily level and braconid wasps (Braconidae), ichneumonid wasps (Ichneumonidae) and wood wasps (Xiphydriidae) to the family level using the identification key of Goulet & Huber (1993). Lepidoptera (belonging to the families Oecophoridae and Tineidae) were identified to species or genus level with the key of [www.lepiforum.de](http://www.lepiforum.de). Thysanoptera were identified to species level and assigned to ecological feeding guilds by Manfred Ullitzka using the keys of (Schliephake & Klimt, 1979; zur Strassen, 2003). Information of the ecological feeding guilds of beetles were gathered from Schmidl & Bussler (2005), Gossner et al. (2013), Horák et al. (2011), Audisio et al. (2014), Seibold et al. (2015), Wende et al. (2017), Bouget et al. (2019), and Hagge et al. (2019) and of flies from Oosterbroek (2006), Ševčík (2010), and [www.diptera.info](http://www.diptera.info).

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**Table S1.** Characteristics of the 25 forests examined in the city of Basel and its surroundings (northwestern Switzerland).

Forest	Coordinates	Forest history <sup>1</sup>	Forest vegetation <sup>2</sup>	Elevation (m a.s.l.)	Exposure <sup>3</sup>	% sealed area (r = 500 m)	Area (ha)	% Forest (r = 500 m)	Fine woody debris (m <sup>3</sup> /ha)	Course woody debris (m <sup>3</sup> /ha)
Bärlauchweglein	47° 34' 7.38" N 7° 39' 4.87" E	Forest	Galio-Fagetum Pulmonarietosum	363	WNW	12	0.8909	55	22.87	7.11
Breite	47° 33' 12.30" N 7° 36' 51.09" E	Fragment	Galio Odorati-Fagetum Cornetosum	262	NE	39	0.7049	3	20.09	13.00
Chrischona	47° 34' 30.78" N 7° 40' 35.28" E	Forest	Galio Odorati-Fagetum Cornetosum	487	–	4	1.4	79	8.98	7.65
Erle	47° 34' 34.58" N 7° 36' 19.23" E	Forest	Galio-Carpinetum Corydalidetosum	269	–	20	2.1	27	6.17	9.69
Friedhof-Rand	47° 33' 50.63" N 7° 38' 42.82" E	Forest	Galio Odorati-Fagetum Pulmonarietosum	319	NNW	12	0.4034	56	10.70	8.11
Fürstensteinerstrasse	47° 32' 12.27" N 7° 36' 5.97" E	Fragment	Galio Odorati-Fagetum Cornetosum	321	NE	54	0.8800	13	10.85	2.31
Geiser	47° 32' 04.6" N 7° 31' 16.2" E	Forest	Galio-Fagetum Pulmonarietosum	351	–	4	52.0	45	17.51	43.43
Glögglhof	47° 34' 53.45" N 7° 38' 51.87" E	Planted	Galio Odorati-Fagetum	283	–	33	0.3135	1	3.25	1.32
Hoelzli	47° 31' 47.76" N 7° 35' 49.19" E	Fragment	Galio Odorati-Fagetum Typicum	370	E	23	2.1	11	13.87	9.18
Hohlweg	47° 35' 15.09" N 7° 40' 2.90" E	Planted	Galio Odorati-Fagetum Typicum	346	S	10	0.2800	21	5.39	4.59
Jakobsbergerholz	47° 31' 57.55" N 7° 36' 11.58" E	Fragment	Galio Odorati-Fagetum Typicum	338	NW	44	1.4	19	7.61	15.68
Klosterfiechten	47° 31' 26.26" N 7° 35' 33.76" E	Fragment	Galio Odorati-Fagetum Typicum	314	–	14	1.94	5	5.74	3.57

Forest	Coordinates	Forest history <sup>1</sup>	Forest vegetation <sup>2</sup>	Elevation (m a.s.l.)	Exposure <sup>3</sup>	% sealed area (r = 500 m)	Area (m <sup>2</sup> )	% Forest (r = 500 m)	Fine woody debris (m <sup>3</sup> /ha)	Course woody debris (m <sup>3</sup> /ha)
Liestal	47° 29' 10.6" N 7° 40' 43.0" E	Forest	Galio-Fagetum Pulmonarietosum	565	–	0	359.0	92	12.99	6.12
Linsberg	47° 34' 25.90" N 7° 39' 53.22" E	Forest	Galio Odorati-Fagetum Cornetosum	450	NW	10	5.0	37	11.83	12.49
Maienbühl	47° 35' 33.14" N 7° 40' 41.10" E	Forest	Galio Odorati-Fagetum Cornetosum	473	SW	3	3.4	54	6.96	4.72
Margarethenpark	47° 32' 30.99" N 7° 35' 2.33" E	Fragment	Galio Odorati-Fagetum Cornetosum	299	NNE	37	1.9	6	13.91	4.91
Mooswäldli	47° 34' 51.72" N 7° 39' 37.41" E	Fragment	Carici Remotae- Fraxinetum Typicum	302	–	16	0.4686	1	9.29	25.88
Muttenz	47° 30' 52.5" N 7° 38' 10.7" E	Forest	Galio-Fagetum Pulmonarietosum	418	–	2	79.0	43	20.52	37.96
Pratteln	47° 30' 31.4" N 7° 40' 04.3" E	Forest	Aro-Fagetum	454	–	2	237.0	66	10.60	9.60
Salamanderweglein	47° 35' 5.71" N 7° 40' 9.23" E	Planted	Galio Odorati-Fagetum Pulmonarietosum	330	SSE	8	0.4061	34	10.40	2.97
Singerstrasse	47° 32' 43.72" N 7° 36' 26.85" E	Planted	Aro-Fagetum	276	–	70	0.1084	2	9.48	8.20
Therwil	47° 30' 18.4" N 7° 34' 46.8" E	Forest	Galio Odorati-Fagetum Typicum	380	–	2	41.0	59	9.68	18.25
Tramwende	47° 34' 20.65" N 7° 37' 11.82" E	Fragment	Galio-Carpinetum Corydalidetosum	265	–	12	0.4576	35	16.37	5.96
Wenkenköppli	47° 34' 29.73" N 7° 39' 29.56" E	Fragment	Galio Odorati-Fagetum Cornetosum	384	NW	12	3.6	26	12.59	24.36
Wolfschlucht	47° 32' 8.70" N 7° 35' 23.09" E	Fragment	Galio Odorati-Fagetum Cornetosum	326	E	31	0.3009	5	12.10	1.81

<sup>1</sup> Forest = Part of a large continuous forest; Fragment = remnant of a former large continuous forest; Planted = forest site was planted after 1884

<sup>2</sup> 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.

<sup>3</sup> Exposure was determined for forest sites situated on a slope.

**Table S2.** Detailed results of GLM analyses examining the effects of degree of urbanisation, forest size, forest500 (percentage of forest in the surrounding 500-m radius), FWD (volume of fine woody debris), c) CWD (volume of coarse woody debris), mean decomposition stage of naturally occurring deadwood, breast height diameter (BHD), branch characteristics including total number of fungal OTUs on branches, moisture content of wood (%), wood pH, and amount of lignin on the number of individuals of total saproxylic individuals and various saproxylic arthropod groups.

	Total saproxylic individuals	Total beetles	Bark beetles	Longhorn beetles	Jewel beetles	Total flies	Dark-winged fungus gnats	Gall midges	Other flies	Moths	Chalcid wasps	Braconid wasps	Ichneumonid wasps
Degree of urbanisation <sup>1</sup>	$F_{1,23}=8.85$ , $p = \mathbf{0.007}$	$F_{1,23}=0.56$ , $p = 0.463$	$F_{1,23}=7.20$ , $p = \mathbf{0.016}$	$F_{1,23}=16.70$ , $p < \mathbf{0.001}$	$F_{1,23}=0.02$ , $p = 0.882$	$F_{1,23}=11.82$ , $p = \mathbf{0.003}$	$F_{1,23}=8.53$ , $p = \mathbf{0.009}$	$F_{1,23}=3.32$ , $p = 0.083$	$F_{1,23}=0.71$ , $p = 0.410$	$F_{1,23}=4.89$ , $p = \mathbf{0.041}$	$F_{1,23}=3.65$ , $p = 0.071$	$F_{1,23}=1.91$ , $p = 0.182$	$F_{1,23}=4.60$ , $p = \mathbf{0.047}$
Forest size <sup>2</sup>	$F_{1,22}=0.53$ , $p = 0.476$	$F_{1,22}=0.28$ , $p = 0.601$	$F_{1,22}=0.06$ , $p = 0.803$	$F_{1,22}=1.05$ , $p = 0.320$	$F_{1,22}=8.07$ , $p = \mathbf{0.010}$	$F_{1,22}=0.72$ , $p = 0.409$	$F_{1,22}=1.02$ , $p = 0.325$	$F_{1,22}=1.83$ , $p = 0.191$	$F_{1,22}=1.16$ , $p = 0.297$	$F_{1,22}=0.04$ , $p = 0.849$	$F_{1,22}=19.66$ , $p < \mathbf{0.001}$	$F_{1,22}=0.21$ , $p = 0.648$	$F_{1,22}=2.23$ , $p = 0.153$
Forest 500 <sup>2</sup>	$F_{1,21}=2.53$ , $p = 0.127$	–	–	–	–	$F_{1,21}=4.57$ , $p = \mathbf{0.047}$	$F_{1,21}=4.30$ , $p = 0.052$	–	$F_{1,21}=3.07$ , $p = 0.098$	$F_{1,21}=2.83$ , $p = 0.111$	–	–	$F_{1,21}=3.09$ , $p = 0.097$
FWD	–	–	$F_{1,21}=1.75$ , $p = 0.203$	$F_{1,21}=12.77$ , $p = \mathbf{0.002}$	–	$F_{1,20}=1.63$ , $p = 0.219$	–	$F_{1,21}=4.36$ , $p = 0.050$	–	$F_{1,20}=3.58$ , $p = 0.076$	–	–	$F_{1,20}=4.28$ , $p = \mathbf{0.054}$
CWD <sup>1</sup>	–	–	–	$F_{1,20}=2.01$ , $p = 0.173$	–	–	–	–	$F_{1,20}=1.45$ , $p = 0.244$	–	$F_{1,21}=1.36$ , $p = 0.259$	–	–

	Total saproxylic individuals	Total beetles	Bark beetles	Longhorn beetles	Jewel beetles	Total flies	Dark-winged fungus gnats	Gall midges	Other flies	Moths	Chalcid wasps	Braconid wasps	Ichneumonid wasps
Decomposition stage	–	$F_{1,21}=12.44$ , <b><math>p = 0.002</math></b>	$F_{1,20}=1.38$ , $p = 0.256$	$F_{1,19}=1.33$ , $p = 0.264$	$F_{1,21}=4.64$ , <b><math>p = 0.044</math></b>	$F_{1,19}=4.14$ , $p = 0.058$	$F_{1,20}=3.28$ , $p = 0.087$	$F_{1,20}=2.68$ , $p = 0.117$	–	–	$F_{1,20}=18.93$ , <b><math>p = 0.003</math></b>	$F_{1,21}=2.70$ , $p = 0.116$	$F_{1,19}=2.93$ , $p = 0.105$
Breast height diameter	–	$F_{1,20}=1.91$ , $p = 0.182$	$F_{1,19}=1.40$ , $p = 0.252$	–	–	–	–	–	–	–	–	–	–
Total number of fungal OTUs	–	–	$F_{1,18}=1.07$ , $p = 0.316$	–	–	–	–	–	$F_{1,19}=1.86$ , $p = 0.190$	$F_{1,19}=1.82$ , $p = 0.195$	–	–	–
Wood moisture content (%)	$F_{1,20}=2.42$ , $p = 0.136$	–	$F_{1,17}=1.51$ , $p = 0.237$	–	$F_{1,20}=1.51$ , $p = 0.235$	$F_{1,18}=4.88$ , <b><math>p = 0.041</math></b>	$F_{1,19}=4.82$ , <b><math>p = 0.042</math></b>	–	$F_{1,18}=14.54$ , <b><math>p = 0.001</math></b>	$F_{1,17}=4.54$ , <b><math>p = 0.048</math></b>	–	–	–
Wood pH	–	–	–	$F_{1,18}=4.48$ , <b><math>p = 0.049</math></b>	$F_{1,19}=3.01$ , $p = 0.099$	$F_{1,17}=2.97$ , $p = 0.103$	$F_{1,18}=2.04$ , $p = 0.170$	–	$F_{1,17}=1.35$ , $p = 0.262$	–	$F_{1,19}=3.81$ , $p = 0.066$	–	$F_{1,18}=3.82$ , $p = 0.067$
Lignin content <sup>1</sup>	–	–	–	–	–	–	–	–	–	$F_{1,16}=1.77$ , $p = 0.201$	–	–	$F_{1,17}=1.76$ , $p = 0.202$

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

<sup>1</sup> = log-transformed variable

<sup>2</sup> = residuals considered because of inter-correlation with degree of urbanisation

**Table S3.** Detailed results of GLM analyses examining the effects of degree of urbanisation, forest size, forest500 (percentage of forest in the surrounding 500-m radius), FWD (volume of fine woody debris), c) CWD (volume of coarse woody debris), mean decomposition stage of naturally occurring deadwood, breast height diameter (BHD), branch characteristics including total number of fungal OTUs on branches, moisture content of wood (%), wood pH, and amount of lignin on the beetle, flies, and moth taxonomic richness.

	Taxonomic richness		
	Beetles	Flies	Moths
Degree of urbanisation <sup>1</sup>	<b><math>Chi^2_{1,23}=1.90</math>, <math>p=0.168</math></b>	<b><math>Chi^2_{1,23}=0.15</math>, <math>p=0.694</math></b>	<b><math>Chi^2_{1,23}=0.11</math>, <math>p=0.739</math></b>
Forest size <sup>2</sup>	<b><math>Chi^2_{1,22}=0.50</math>, <math>p=0.480</math></b>	<b><math>Chi^2_{1,22}=0.01</math>, <math>p=0.911</math></b>	<b><math>Chi^2_{1,22}=0.22</math>, <math>p=0.642</math></b>
Forest 500 <sup>2</sup>	–	–	–
FWD	<b><math>Chi^2_{1,21}=1.42</math>, <math>p=0.233</math></b>	–	–
CWD <sup>1</sup>	–	–	–
Decomposition stage	<b><math>Chi^2_{1,20}=1.64</math>, <math>p=0.201</math></b>	–	–
Breast height diameter	–	–	–
Total number of fungal OTUs	–	–	<b><math>Chi^2_{1,23}=1.16</math>, <math>p=0.281</math></b>
Wood moisture content (%)	–	<b><math>Chi^2_{1,21}=1.06</math>, <math>p=0.302</math></b>	–
Wood pH	–	–	–
Lignin content <sup>1</sup>	–	–	–

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

<sup>1</sup> = log-transformed variable

<sup>2</sup> = residuals considered because of inter-correlation with degree of urbanisation

**Table S4.** Table depicting all identified saproxylic individuals assigned to their ecological feeding guilds. The saproxylic individuals were classified into 5 feeding guilds. 1) mycetophagous (consuming fungi or mouldy material), 2) saprophagous (feeding on decaying organic material), 3) xylophagous (primary consumers of woody material), 4) predatory (predators on other saproxylics), and 5) parasitic (developing within other saproxylic larvae or parasitoid larvae feed externally on saproxylics).

The ecological feeding guilds information for the beetles were derived from Schmidl & Bussler (2005), Horak et al. (2011); Gossner et al. (2013); Audisio et al. (2014); Seibold et al. (2015); Wende et al. (2017); Bouget et al. (2019); Hagge et al. (2019). Beetles that were not present in the German list (Schmidl & Bussler, 2005) or German databases/publications but were present in the Italian (Audisio et al., 2014) or French (Bouget et al., 2019) saproxylic red lists, or in Horak et al. (2011) were included as saproxylic beetles. The ecological feeding guilds for Thysanoptera were obtained from Schliephake & Klimt (1979) and zur Strassen (2003), those for flies from Oosterbroek (2006), Sevcick (2010) and [www.diptera.info](http://www.diptera.info). The Hymenoptera were assigned to feeding guilds following Goulet & Huber (1993). The other insects were assigned to feeding guilds following Stresemann (2011). The articles cited in this table are listed in the reference list of Appendix S1.

Insect group	Species/Genus/Sub-family/Family/Superfamily	Ecological feeding guild	Number of individuals
Curculionidae	<i>Acalles micros</i>	xylophagous	2
Curculionidae	<i>Kykliaacalles roboris</i>	xylophagous	4
Curculionidae	<i>Trachodes hispidus</i>	xylophagous	17
Curculionidae	<i>Magdalis flavicornis</i>	xylophagous	1
Curculionidae	<i>Rhyncolus ater</i>	xylophagous	2
Curculionidae	<i>Euophryum confine</i>	xylophagous	1
Curculionidae Scolytinae	<i>Taphrorychus bicolor</i>	xylophagous	14401
Curculionidae Scolytinae	<i>Ernoporicus fagi</i>	xylophagous	657
Curculionidae Scolytinae	<i>Scolytus intricatus</i>	xylophagous	2508
Curculionidae Scolytinae	<i>Xylosandrus germanus</i>	mycetophagous	31
Curculionidae Scolytinae	<i>Xyleborus monographus</i>	mycetophagous	58
Salpingidae	<i>Salpingus ruficollis</i>	predatory	2
Salpingidae	<i>Salpingus planirostris</i>	predatory	61
Salpingidae	<i>Vincenzellus ruficollis</i>	predatory	4
Cleridae	<i>Opilo molis</i>	predatory	2
Elateridae	<i>Ampedus sanguinolentus</i>	xylophagous	1
Laemophloeidae	<i>Laemophloeus monilis</i>	Predatory larvae	1
Laemophloeidae	<i>Placonotus testaceus</i>	Predatory larvae	3
Laemophloeidae	<i>Cryptolestes duplicatus</i>	Predatory larvae	11

<b>Insect group</b>	<b>Species/Genus/Sub-family/Family/Superfamily</b>	<b>Ecological feeding guild</b>	<b>Number of individuals</b>
Silvanidae	<i>Uleiota planata</i>	predatory	26
Silvanidae	<i>Silvanus unidentatus</i>	predatory	51
Silvanidae	<i>Silvanus bidentatus</i>	predatory	41
Monotomidae	<i>Rhizophagus bipustulatus</i>	predatory	9
Monotomidae	<i>Rhizophagus perforatus</i>	predatory	1
Monotomidae	<i>Monotoma longicollis</i>	mycetophagous	1
Trogositidae	<i>Nemozoma elongatum</i>	predatory	22
Anthribidae	<i>Platystomos albinus</i>	xylophagous	2
Anthribidae	<i>Pseudeuparius sepicola</i>	xylophagous	1
Melyridae	<i>Dasytes plumbeus</i>	predatory	33
Melyridae	<i>Dasytes aeratus</i>	predatory	1
Melyridae	<i>Daystes caeruleseus</i>	predatory	11
Scraptiidae	<i>Anaspis flava</i>	xylophagous	19
Scraptiidae	<i>Anaspis frontalis</i>	xylophagous	1
Anobiidae	<i>Anobium punctatum</i>	xylophagous	1
Anobiidae	<i>Hemicoelus fulvicornis</i>	xylophagous	1
Anobiidae	<i>Xestobium plumbeum</i>	xylophagous	1
Anobiidae	<i>Ernobius angusticollis</i>	xylophagous	1
Mycetophagidae	<i>Litargus connexus</i>	mycetophagous	430
Mycetophagidae	<i>Mycetophagus atomarius</i>	mycetophagous	2
Mycetophagidae	<i>Typhaea stercorea</i>	mycetophagous	2
Mycetophagidae	<i>Berginus tamarisci</i>	mycetophagous	3
Zoopheridae	<i>Synchita undata</i>	mycetophagous	1
Malachiidae	<i>Sphinginus lobatus</i>	Predatory larvae	1
Throscidae	<i>Aulonothroscus brevicollis</i>	saprophagous scavenger	17
Nitidulidae	<i>Epuraea rufomarginata</i>	mycetophagous	2
Leiodidae	<i>Anisotoma</i> sp.	mycetophagous	1
Corylophidae	<i>Arthrolips</i> sp.	mycetophagous	1
Corylophidae	<i>Sericoderus lateralis</i>	saprophagous scavenger	4534
Latridiidae	<i>Corticaria</i> sp.	mycetophagous	8
Latridiidae	<i>Stephostethus alternans</i>	mycetophagous	3
Latridiidae	<i>Dienerella clathrata</i>	mycetophagous	10
Latridiidae	<i>Cartodere nodifer</i>	mycetophagous	221

<b>Insect group</b>	<b>Species/Genus/Sub-family/Family/Superfamily</b>	<b>Ecological feeding guild</b>	<b>Number of individuals</b>
Latriviidae	<i>Latridius</i> sp.	mycetophagous	93
Cryptophagidae	<i>Atomaria</i> sp.	mycetophagous	255
Cryptophagidae	<i>Cryptophagus</i> sp.	mycetophagous	11386
Cerambycidae	<i>Pogonocherus hispidulus</i>	xylophagous	230
Cerambycidae	<i>Leiopus nebulosus</i> aggr.	xylophagous	392
Cerambycidae	<i>Mesosa nebulosa</i>	xylophagous	6
Cerambycidae	<i>Clytus arietis</i>	xylophagous	1
Cerambycidae	<i>Xylotrechus antilope</i>	xylophagous	1
Cerambycidae	<i>Phymatodes testaceus</i>	xylophagous	126
Cerambycidae	<i>Grammoptera ruficornis</i>	xylophagous	4
Cerambycidae	<i>Anaesthetis testacea</i>	xylophagous	1
Buprestidae	<i>Agrilus angustulus</i>	xylophagous	522
Buprestidae	<i>Agrilus sulcicollis</i>	xylophagous	11
Buprestidae	<i>Agrilus olivicolor</i>	xylophagous	926
Buprestidae	<i>Agrilus graminis</i>	xylophagous	2
Staphylinidae	<i>Phloeocharis subtilissima</i>	predatory	10
Staphylinidae	<i>Phloeonomus punctipennis</i>	predatory	16
Staphylinidae	<i>Carpelimus gracilis</i>	saprophagous	1
Staphylinidae	<i>Tachyporus obtusus</i>	predatory	1
Staphylinidae	<i>Oligota granaria</i>	predatory	25
Staphylinidae	<i>Oligota parva</i>	predatory	3
Staphylinidae	<i>Cypha apicalis</i>	predatory	1
Staphylinidae	<i>Anomognathus cuspidatus</i>	predatory	11
Staphylinidae	<i>Leptusa fumida</i>	predatory	7
Staphylinidae	<i>Leptusa ruficollis</i>	predatory	22
Staphylinidae	<i>Atheta coriaria</i>	predatory	304
Staphylinidae	Pselaphinae sp.	predatory	1
Carabidae	<i>Dromius quadrimaculatus</i>	predatory	7
<b>Parasitoid wasps</b>			
Chalcidodea	Chalcid wasps	parasitoid	5148
Braconidae	Braconid wasps	parasitoid	5675
Ichneumonidae	Ichneumonid wasps	parasitoid	431

Insect group	Species/Genus/Sub-family/Family/Superfamily	Ecological feeding guild	Number of individuals
<b>Moths</b>			
Oecophoridae	<i>Oecophora bractella</i>	mycetophagous	30
Oecophoridae	<i>Metalampra italica</i>	mycetophagous	1299
Oecophoridae	<i>Shiffermuelleria schaefferella</i>	mycetophagous	2
Oecophoridae	<i>Epicallima formosella</i>	mycetophagous	23
Tineidae	<i>Nemapogon</i> spp.	mycetophagous	201
<b>Diptera</b>			
Cecidomyiidae	Sub-family Lestremiinae and Micromyiinae (wood midges)	mycetophagous	44474
Sciaridae	<i>Trichosia</i> sp.	mycetophagous	88230
Mycetophilidae		mycetophagous	466
Phoridae	<i>Megaselia</i> sp.	unknown	181
Drosophilidae	<i>Stegana</i> sp.	saprophagous	91
Chloropidae	<i>Gaurax fascipes</i>	mycetophagous	187
Scatopsidae	<i>Coboldia fuscipes</i>	saprophagous	2787
Syrphidae	<i>Cheilosia longula</i>	mycetophagous	1
Tipulidae		phyto saprophagous	1
Anthomyiidae		saprophage	28
Stratiomyidae	<i>Pachygaster atra</i>	predatory necrophagous	1
Dolichopodidae	<i>Medetera</i> sp.	predatory	56
Lauxaniidae	<i>Homoneura interstincta</i>	Saprophagous	2
<b>Saproxylic Heteroptera</b>			
Anthocoridae	<i>Xylocoris cursitans</i>	predatory	215
Aradidae	<i>Aneurus laevis</i>	mycetophagous	1
<b>Other saproxylics</b>			
Psocoptera	<i>Caecilius fuscopterus</i> and <i>Trichadenotecnum</i> sp.	phyto saprophagous	6324
Thysanoptera	<i>Xylaplothrips fulginosus</i>	mycetophagous	4
Thysanoptera	<i>Hoplothrips corticis</i>	mycetophagous	23
Thysanoptera (Phlaeothripidae)	<i>Poecilothrips albopictus</i>	mycetophagous	44

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<b>Insect group</b>	<b>Species/Genus/Sub-family/Family/Superfamily</b>	<b>Ecological feeding guild</b>	<b>Number of individuals</b>
Thysanoptera	<i>Aeolothrips versicolor</i>	predatory	1
Raphidioptera		predatory	1
Neuroptera	larvae	predatory	2
Xiphydriidae		xylophagous	14
<b>Total number of saproxylic insect individuals</b>			<b>193534</b>

**Table S5.** Results of GLM analyses examining the effects of degree of urbanisation, forest size, forest500 (percentage of forest within a radius of 500 m), FWD (volume of fine woody debris), CWD (volume of coarse woody debris), mean decomposition stage of naturally occurring deadwood, breast height diameter (BHD), branch characteristics including total number of fungal OTUs on branches, moisture content of wood (%), wood pH, and amount of lignin on the proportion of insect individuals belonging to different feeding guilds.

	Proportion of mycetophagous individuals	Proportion of saprophagous individuals	Proportion of all xylophagous individuals	Proportion of all predatory individuals	Proportion of parasitic wasps
Degree of urbanisation <sup>1</sup>	$F_{1,23}=3.29$ , $p = 0.088$	$F_{1,23}=24.48$ , <b><math>p &lt; 0.001</math></b>	$F_{1,23}=0.29$ , $p = 0.596$	$F_{1,23}=0.002$ , $p = 0.962$	$F_{1,23}=0.24$ , $p = 0.630$
Forest size <sup>2</sup>	$F_{1,22}=1.18$ , $p = 0.293$	$F_{1,22}=18.47$ , <b><math>p &lt; 0.001</math></b>	$F_{1,22}=0.0002$ , $p = 0.990$	$F_{1,22}=0.72$ , $p = 0.407$	$F_{1,22}=0.41$ , $p = 0.532$
Forest 500 <sup>2</sup>	$F_{1,21}=6.12$ , <b><math>p = 0.025</math></b>	$F_{1,21}=8.25$ , <b><math>p = 0.011</math></b>	$F_{1,21}=1.01$ , $p = 0.328$	–	$F_{1,21}=1.10$ , $p = 0.306$
FWD	$F_{1,20}=3.13$ , $p = 0.096$	–	$F_{1,20}=1.35$ , $p = 0.262$	$F_{1,21}=1.29$ , $p = 0.271$	–
CWD <sup>1</sup>	$F_{1,19}=1.63$ , $p = 0.220$	$F_{1,20}=4.18$ , $p = 0.057$	–	–	–
Decomposition stage	$F_{1,18}=16.99$ , <b><math>p &lt; 0.001</math></b>	$F_{1,19}=10.81$ , <b><math>p = 0.004</math></b>	$F_{1,19}=3.05$ , $p = 0.099$	$F_{1,20}=2.00$ , $p = 0.174$	$F_{1,20}=6.36$ , <b><math>p = 0.020</math></b>
Breast height diameter	–	–	–	–	–
Total number of fungal OTUs	–	–	–	–	–
Wood moisture content (%)	$F_{1,17}=12.52$ , <b><math>p = 0.003</math></b>	$F_{1,17}=9.35$ , <b><math>p = 0.007</math></b>	$F_{1,18}=3.88$ , $p = 0.065$	$F_{1,19}=2.63$ , $p = 0.122$	–
Wood pH	$F_{1,16}=2.43$ , $p = 0.139$	–	$F_{1,17}=2.43$ , $p = 0.137$	$F_{1,18}=2.57$ , $p = 0.127$	–
Lignin content <sup>1</sup>	–	$F_{1,17}=1.19$ , <b><math>p = 0.290</math></b>	–	–	–

– Factor was excluded from the model due to the step-wise reduction procedure

Significant effects ( $P < 0.05$ ) are presented in bold

<sup>1</sup> = log-transformed variable

<sup>2</sup> = residuals considered because of inter-correlation with degree of urbanisation

**Table S6.** Detailed results of GLM analyses examining the effects of degree of urbanisation, forest size, forest500 (percentage of forest in the surrounding 500-m radius), FWD (volume of fine woody debris), c) CWD (volume of coarse woody debris), mean decomposition stage of naturally occurring deadwood, breast height diameter (BHD), branch characteristics including total number of fungal OTUs on branches, moisture content of wood (%), wood pH, and amount of lignin on the proportion of total and beetle mycetophagous, saprophagous, xylophagous, and predatory taxonomic richness.

	Proportion of taxonomic richness							
	Total mycetophagous	Mycetophagous beetles	Total saprophagous	Saprophagous beetle	Total xylophagous	Xylophagous beetles	Total predatory	Predatory beetles
Degree of urbanisation <sup>1</sup>	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.16, <i>p</i> =0.687	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =1.38, <i>p</i> =0.240	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.86, <i>p</i> =0.354	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.56, <i>p</i> =0.455	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =1.02, <i>p</i> =0.312	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.97, <i>p</i> =0.324	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.17, <i>p</i> =0.682	<i>Chi</i> <sup>2</sup> <sub>1,23</sub> =0.25, <i>p</i> =0.617
Forest size <sup>2</sup>	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.10, <i>p</i> =0.755	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.80, <i>p</i> =0.372	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.73, <i>p</i> =0.394	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.002, <i>p</i> =0.963	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.02, <i>p</i> =0.891	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =0.06, <i>p</i> =0.806	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =1.45, <i>p</i> =0.229	<i>Chi</i> <sup>2</sup> <sub>1,22</sub> =1.10, <i>p</i> =0.294
Forest 500 <sup>2</sup>	–	–	–	–	–	–	–	<i>Chi</i> <sup>2</sup> <sub>1,21</sub> =1.07, <i>p</i> =0.302
FWD	–	–	–	–	–	–	–	–
CWD <sup>1</sup>	–	–	–	–	–	–	–	–
Decomposition stage	–	–	–	–	–	–	–	–
Breast height diameter	–	–	–	<i>Chi</i> <sup>2</sup> <sub>1,21</sub> =1.28, <i>p</i> =0.257	–	–	–	–
Total number of fungal OTUs	–	–	<i>Chi</i> <sup>2</sup> <sub>1,21</sub> =1.19, <i>p</i> =0.276	–	–	–	–	–
Wood moisture content (%)	–	–	–	–	–	–	–	–
Wood pH	–	–	–	–	–	–	–	–
Lignin content <sup>1</sup>	–	–	–	–	–	–	–	–

– Factor was excluded from the model due to the step-wise reduction procedure, Significant effects ( $P < 0.05$ ) are presented in bold,

<sup>1</sup> = log-transformed variable, <sup>2</sup> = residuals considered because of inter-correlation with degree of urbanisation

**Table S7.** Summary of the GLM analyses examining the effects of degree of urbanisation, forest size, forest500 (percentage of forest in the surrounding 500-m radius), FWD (volume of fine woody debris), c) CWD (volume of coarse woody debris), decomposition stage of naturally occurring deadwood, breast height diameter (BHD), branch characteristics including moisture content of wood (%), wood pH and lignin content on the number of total fungal species (OTUs) on the branches exposed and separately the number of fungal species on both the beech and oak branches exposed in the 25 forests.

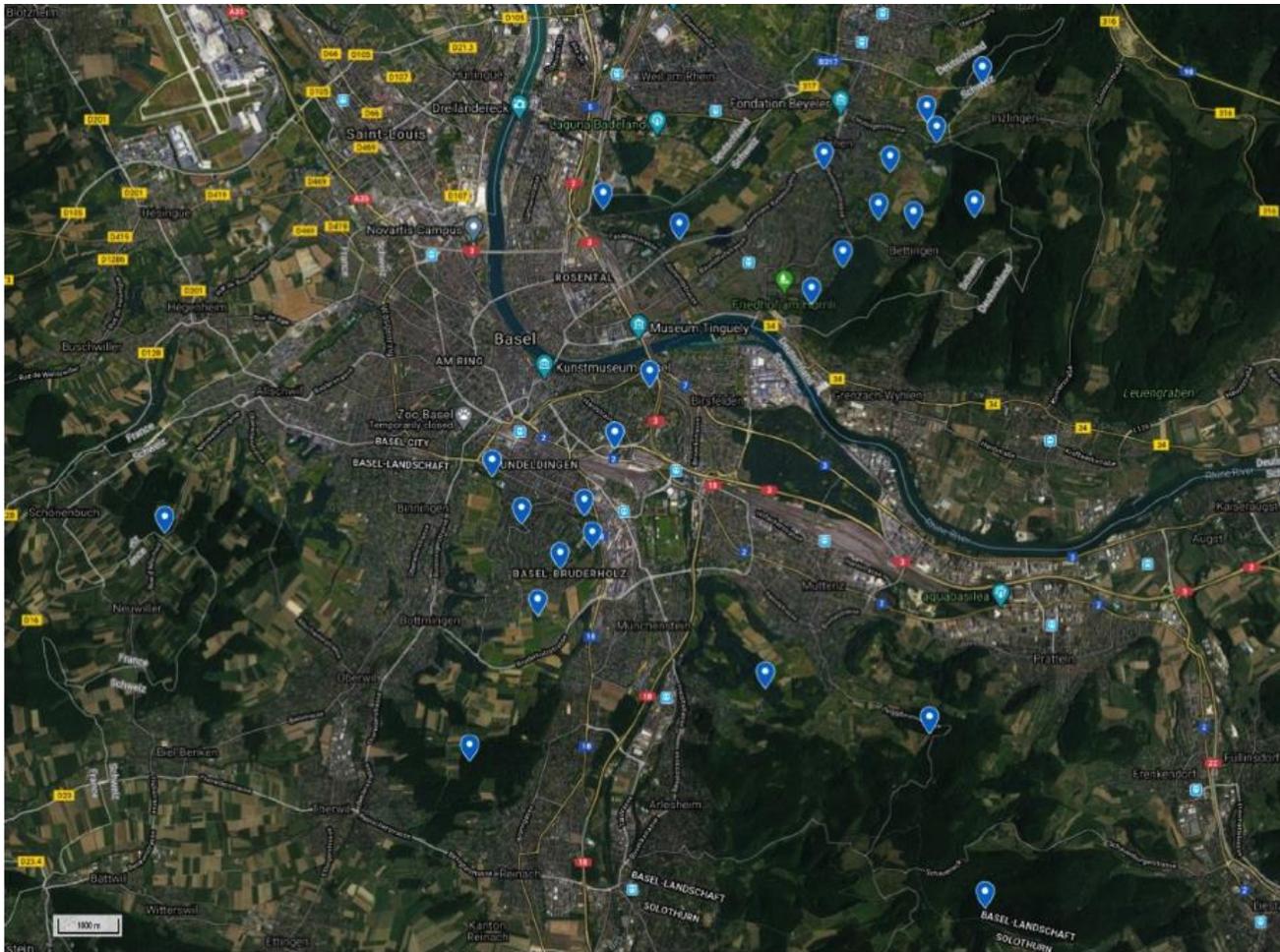
	Total number of fungal species (OTUs) on the branch bundles <sup>1</sup>	Number of fungal species (OTUs) on beech branches <sup>1</sup>	Number of fungal species (OTUs) on oak branches <sup>1</sup>
Degree of urbanisation	$Chi^2_{1,23}=6.31, p = \mathbf{0.012}$	$Chi^2_{1,23}=0.90, p = 0.342$	$Chi^2_{1,23}=8.84, p = \mathbf{0.003}$
Forest size	$Chi^2_{1,22}=0.98, p = 0.323$	$Chi^2_{1,22}=1.61, p = 0.204$	$Chi^2_{1,22}=1.12, p = 0.290$
Forest 500	$Chi^2_{1,21}=2.00, p = 0.157$	–	$Chi^2_{1,21}=3.01, p = 0.083$
FWD	$Chi^2_{1,20}=4.21, p = \mathbf{0.040}$	$Chi^2_{1,21}=2.14, p = 0.144$	$Chi^2_{1,20}=4.91, p = \mathbf{0.027}$
CWD	–	–	–
Decomposition stage	–	–	–
Breast height diameter	–	–	–
Wood moisture content (%)	–	$Chi^2_{1,20}=1.45, p = 0.229$	–
Wood pH	–	–	–
Lignin content	–	$Chi^2_{1,19}=1.31, p = 0.253$	–

<sup>1</sup> = GLM model with poisson distributed errors

<sup>2</sup> = GLM model with quasipoisson distributed errors

– Factor was excluded from the model due to the step-wise reduction procedure

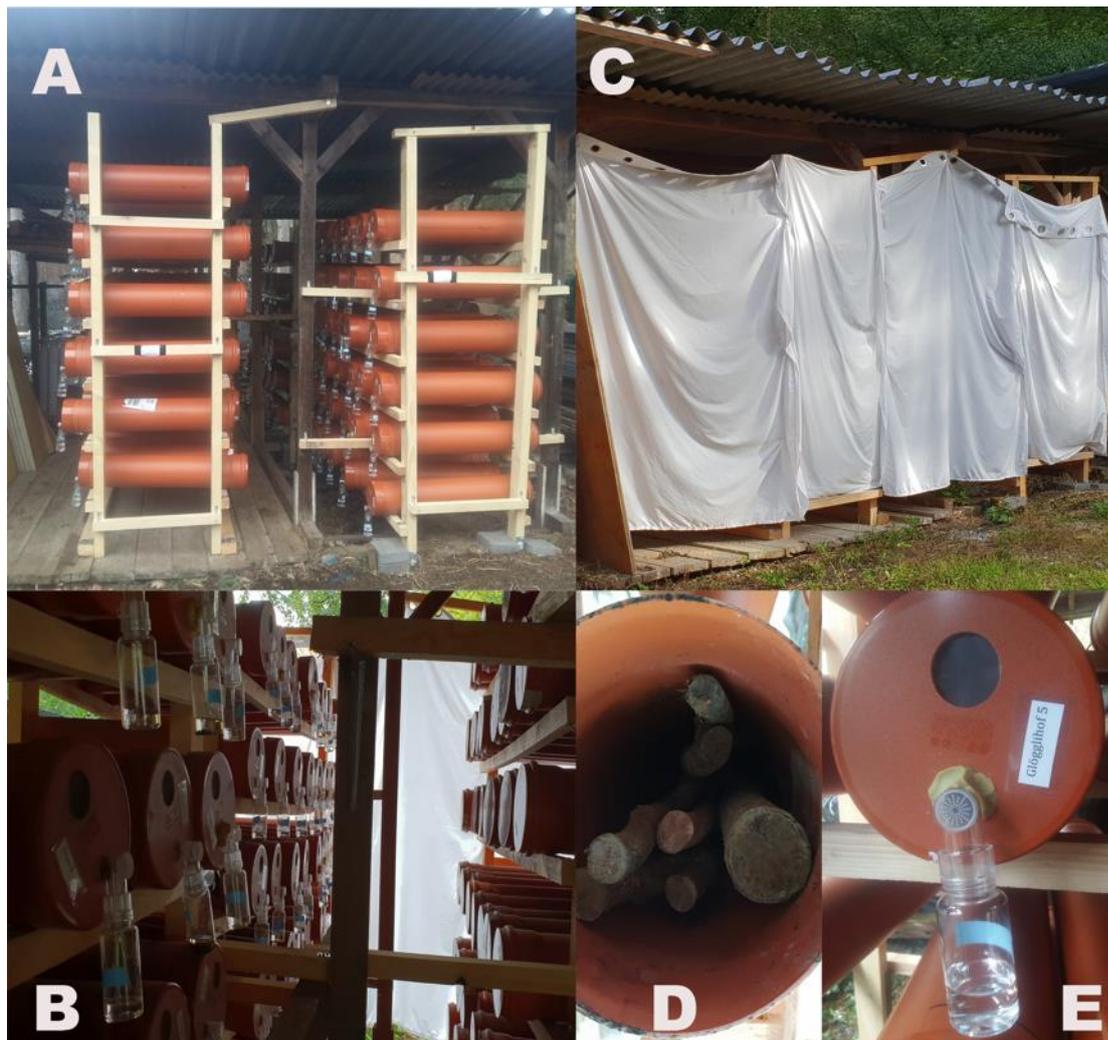
Significant effects ( $P < 0.05$ ) are presented in bold



**Figure S1** The 25 forest sites (marked in dark blue) that were investigated in Basel and surroundings situated in varying degrees of urbanisation and consisting of a range of forest sizes (Source: Google Earth, 07.2018).



**Figure S2** Branch bundle attached to a beech stem at a height of 1.5 m.



**Figure S3. Emergence traps.** A), B) emergence traps wooden frame. C) white cloth in front of the emergence traps to block off the direct midday sunlight, D) branches within an emergence trap, and E) the lid set up of the emergence trap with a 51 mm hole covered with 0.5 mm mesh size for ventilation and the collection bottle (FJ Technology Co., Ltd.) with 70% ethanol, which was emptied and refilled every month.

## GENERAL DISCUSSION

Urbanisation can lead to major changes in the remaining green areas, including altered environmental conditions, fragmentation and increased isolation of habitats (New et al. 2015). Remaining habitat patches are reduced in size and exhibit more pronounced edge effects than large patches (e.g. higher temperatures and lower humidity; Dale and Frank 2014). Urbanisation-induced changes in biotic and abiotic conditions can create novel ecosystems with a distinct species composition and altered ecosystem processes (McDonnell and Hahs 2015). Species richness and species composition of urban habitat patches are mainly determined by their quality and size (Beninde et al. 2015; Melliger et al. 2017b; 2018). In addition, the landscape surrounding the habitat plays an important role for both species richness and composition (Lepczyk et al. 2017). Because forest arthropods are seemingly impacted by rising urban pressures (Magura et al. 2013; Melliger et al. 2018), we expected that an increasing degree of urbanisation and decreasing forest size would negatively influence the abundance of arthropods associated with living tree species and decaying organic material (litter and deadwood).

In **Chapter I**, I investigated the effects of degree of urbanisation and forest size on plant galling infestation rates and herbivorous leaf damage by arthropods. Similar to other studies (Raupp et al. 2010; Piano et al. 2020), I found species- and/or taxon-specific responses to the degree of urbanisation and forest size. Regarding plant-galling arthropods, I recorded the highest infestation rates in sycamore and beech trees growing in forests in low urbanised areas. The beech gall midge *Mikiola fagi* was the only species which responded to the degree of urbanisation. Furthermore, smaller forests had drastically reduced infestation rates of total beech galls and that of *Mikiola fagi* than large forests. This pattern could be due to the lower proportion of beech trees in smaller forests than in larger ones. The large beech-dominated forests in the sub-urban areas around Basel city provide abundant resources for galling arthropods that are specific on beech trees as hosts (Mangels et. 2015). Other local forest characteristics including reduced litter biomass in small forests could have increased the mortality of overwintering beech gallers (Segebadé and Schaefer 1979). I also recorded urbanisation and forest size effects on damaged sycamore leaves by herbivores. The highest total leaf damage on sycamore was found in highly urbanised areas, and the lowest in small forests. Leaves of urban trees can have a higher nutrient concentration (phosphorus and nitrogen) and reduced leaf chemical defences (phenolic compounds) than leaves in rural areas, which theoretically should make them more susceptible to herbivore damage (Moreira et al. 2019). However, as recently reported by Moreira et al. (2019), there might still be a reduced chewing arthropod damage in urban areas. This suggests that these herbivores are rather negatively affected by other factors associated with urbanisation like fragmentation,

habitat isolation and altered environmental conditions (Martinson and Fagan 2014) and/or higher predator pressure in urban areas (Turrini et al. 2016; Kozlov et al. 2017; Moreira et al. 2019).

In contrast to the antagonistic relationships of herbivorous arthropods and their host trees in forests (**Chapter I**), I focused in **Chapter II** on ground-dwelling arthropods that are essential for leaf litter decomposition. Similar to a previous study conducted in Basel (Melliger et al. 2017a), there was a negative effect of increasing degree of urbanisation on litter decomposition rates ( $k_{\text{litter}}$ ), which is most likely driven by the reduced soil moisture content in urban forests that in turn may reduce microbial activity and its biomass involved in breaking down litter (Malmivaara-Lämsä et al. 2008; Melliger et al. 2017a; Petraglia et al. 2019). The exclusion of litter organisms with different mesh sizes of litterbags revealed that bags with large mesh size have the highest decomposition rates because of the combined effects of increased leaching of leaf litter and the activity of larger soil arthropods (e.g. earthworms; Kampichler and Bruckner 2009; Bokhorst and Wardle 2013). The similar decomposition rates recorded in medium-sized and small mesh bags could be an effect of the high activity of bacteria and fungi (Purahong et al. 2016). In terms of the litter meso-fauna (body size: 200  $\mu\text{m}$ –2 mm; dominated by oribatid mites and Collembola), there were contrasting results in response to degree of urbanisation and forest size. While Acari were most abundant in forests situated in moderately urbanised areas, Collembola were most abundant in forests in highly urbanised areas. The high abundances of Acari and Collembola in urban forests suggest that their communities are fairly tolerant to anthropogenic pressure like soil/litter disturbance and are dominated by ubiquitous species that may benefit from reduced interspecific competition in urban areas (Maraun et al. 2003; Santorufo et al. 2014; Mangová et al. 2019).

The study presented in **Chapter III** demonstrates the impact of urbanisation on deadwood-dependent (saproxylic) insects and fungi. I investigated a wide variety of saproxylic insect groups that constitute various ecological feeding guilds. I found that total saproxylic individuals, bark and longhorn beetles and mycetophagous (fungi-feeding) flies responded negatively to an increasing degree of urbanisation. Many of these taxa are pioneers searching for fresh deadwood. These pioneers have excellent flying abilities and are not bound to local amount of deadwood (Gossner et al. 2013). Therefore, landscape factors such as the degree of urbanisation may make it difficult for these insects to locate and aggregate on fresh beech or oak deadwood in a fragmented urban matrix (Piel et al. 2005). At a finer scale, the choice of food and oviposition sites of saproxylic insect are based on deadwood characteristics such as tree species, deadwood diameter, decay stage, wood moisture content, wood lignin and wood pH (Vanderwel et al. 2006; Seibold et al. 2015). Indeed I found that an increase in wood moisture of the branches caused a shift in the total taxonomic composition

of insects and promoted flies and mycetophagous individuals that were able to increase their individual numbers exponentially because of optimal branchwood conditions. An increase in the degree of urbanisation can alter taxonomic composition of various arthropods as shown in moths (Piano et al. 2020) and carabid beetles (Niemelä and Kotze 2009). I could also demonstrate that urbanisation caused a shift in the taxonomic composition of beetles and fungal OTUs. Networks and food webs in urban areas that exhibit changes in interactions between partners often leads to a higher generalisation (Geslin et al. 2013; Start et al. 2020). In my study the shifts in species composition resulted in alterations in insect–fungi interactions.

The three studies highlight the necessity to investigate several taxa at the same time because their responses can vary greatly due to differences in life histories and sensitivities to landscape and local forest variables.

### **Implications and Outlook**

Insects are impacted by anthropogenic activities ranging from climate change to land-use changes including the expansion of urban areas. Recent studies have shown that insect declines are prevalent throughout Europe and North America (van Klink et al. 2020; Wagner et al. 2020). Therefore, it is important to understand the processes and drivers of these declines. This may help us to mitigate any further declines by effective management of semi-natural habitats and other measures.

The negative effects of increasing degree of urbanisation and decreasing forest size on some arthropods shown in this thesis (e.g. plant galling infestation rates: **Chapter I**; saproxylic insect abundance and fungi richness: **Chapter III**) reiterates the importance of landscape structure. Improving the connectedness between habitat patches by providing “stepping stones” of resources (e.g. deadwood) or corridors in form of vegetation strips may enhance insect dispersal within an urban matrix (Beninde et al. 2015). In addition, maintaining large habitats can be essential to support area-sensitive species such as forest specialists (Magura et al. 2013; Beninde et al. 2015).

Nevertheless, several species or taxa did not respond to urbanisation and forest size in my thesis (e.g. galling and herbivorous arthropods on ash leaves; **Chapter I**) or even showed increased abundances (e.g. Collembola) in forests situated in highly urbanised areas (**Chapter II**). As Sattler et al. (2011) proclaimed, urban areas should not be viewed as a threat to biodiversity, but rather as an opportunity. With the right provisioning of resources and management of semi-natural habitats, urban areas cannot only harbour arthropods occurring in the surrounding landscape, but may even promote a distinct composition of arthropods, especially thermophilous species including otherwise rare species (e.g. grassland weevils in

Swiss cities; Germann et al. 2008).

In the future, foresters and owners of urban forests will increasingly face challenges such as a high frequency of heat waves and the associated heat-stress on trees (Ma et al. 2020; Schuldt et al. 2020). Furthermore, foresters and forest owners have to meet the demands of human recreation, to manage the forest so that the key ecosystem services can be provided, and to promote biodiversity (Niemelä et al. 2010; Escobedo et al. 2011). However, there is hope for optimism that conservation efforts can have a certain impact even in heavily altered landscapes in western Europe. This was shown in the case of pollinators, where targeted provisioning of floral and nesting resources have slowed down the decline of and even reversed some of the declines of wild bees in the United Kingdom and the Netherlands (Carvalho et al. 2013).

Regarding the studies in my thesis, simple measures like allowing the litter layer to accumulate in urban forests can be beneficial for the litter and soil fauna (**Chapter II**) and several arthropods (including plant-galling arthropods) to use the litter layer as overwintering habitat (**Chapter I**). In terms of logging, a city provides challenges for foresters due to the increased pressures of making a forest secure for the citizens using it for recreation (Fröhlich and Ciach 2020). Old dying trees sometimes have to be cut down due to fear of falling onto footpaths or houses. However, when a tree is several metres away from a footpath or a building, then it is possible to cut it at several metres height and leave it as a snag, which provides suitable habitat and refuge for many saproxylics that require several years to develop before they hatch (Jonsell and Weslin 2003; Bouget et al. 2012). This fairly simple measure seems to have also reached the Basel foresters as I witnessed a couple of these snags in the forests investigated (**Chapter III**). Another simple measure observed in these forests is the piling up of branches left after logging, which might help to sustain common fungi (Pasanen et al. 2014) and benefit other saproxylics in the forests (Jonsell et al. 2007). The decision to leave some deadwood of different sizes lying around after a wood harvest or after a storm supports common species (Hottola et al. 2009) and may eventually promote saproxylics in managed forests of Basel (Pasanen et al. 2014; Roth et al. 2019).

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