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ORIGINAL ARTICLE

Detritus-filled crotches – an overlooked tree-related microhabitat in Central Europe

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Abstract. In the field of biodiversity research, tree-related microhabitats in the temperate zone have received substantial interest in the last decade, but one particular microhabitat type, crown microsoils in tree crotches, has largely escaped the attention of scientists. We present a study from Central Europe that focused on the meso- and macrofauna in this microhabitat type. In twelve crotches we found more than 3000 individual animals out of 14 orders, encompassing all major elements of the terrestrial soil decomposer food web. Collembola accounted for more than 50% of the total. As expected, taxon richness correlated with habitat size. We conclude that this is an ideal natural system to study fundamental ecological questions of faunal community assembly.

INTRODUCTION

Foundation species (Ellison, 2019) or ecosystem engineers (Jones et al., 1994) are organisms that create habitats by physically changing the abiotic or biotic conditions for other species. The resulting increase in habitat diversity typically leads to an increase in local biodiversity (Thomsen et al., 2018, 2022). Trees are a prime example of such foundation species (Jones et al., 1997). Tree-related Microhabitats (hereafter TreMs) are essential for a considerable number of plants, animals and fungi (e.g. Kraus et al., 2016; Courbaud et al., 2017; Larrieu et al., 2018; Bütler et al., 2020). Arthropods are the most diverse component of terrestrial ecosystems (Kremen et al., 1993), with a large number of taxa associated with TreMs (Larrieu et al., 2018). There are numerous forms of TreMs, such as cavities, crown dead wood, excrescences, or epiphytic structures: a detailed account of these microhabitats can be found in Larrieu et al. (2018). The frequency and diversity of TreMs depends on tree age, tree diameter, and tree species identity (Bütler et al., 2020). One type, concavities, frequently develop within the crotches (multiple opposite branches or trunks) of sycamore maple (*Acer pseudoplatanus* L.), but can also be observed in other tree species, e.g. Norway maple (*Acer platanoides* L.) (Hoeber & Zotz, 2021), and are induced by tree growth (Jones et al., 1997). *Acer* trees are initially monopodial with opposite buds and the entire main stem develops out of a single growing point. When this leading shoot is hampered in growth for any reason, the trees often start growing again from two axes, reflecting the opposite buds (Sieghardt et al., 2005). Due to the frequent observation of this response in *Acer* trees (Hoeber & Zotz, 2021), we suggest that such disturbances commonly occur in *Acer* and that they subsequently initiate the development of concavities. Organic material, e.g. leaves or pieces of bark, that accumulates in crotches leads to the formation of "crown microsoil", one of the described structures in Larrieu et al. (2018). Crown microsoils can support high levels of species diversity (Dourson & Dourson, 2006), harboring distinct assemblages of collembolans (Rodgers & Kitching, 1998, 2011), oribatid (Lindo & Winchester, 2005) and gamasid mites (Beaulieu et al., 2010), in comparison to ground soils. This makes them an ideal system for studying biodiversity and nature conservation that is currently underused (Martin et al., 2022). Larrieu et al. (2018) state that knowledge of the communities associated with crown microsoils is relatively scarce for temperate and Mediterranean forests. This statement is somewhat surprising because there is a relatively rich literature on crown microsoils and the associated fauna from temperate rainforests in Chile, North America and New Zealand (Wardle et al., 2003; Enloe et al., 2006; Armesto et al., 2009). Additionally, further research has been published on crown microsoils in tropical systems (Beaulieu et al., 2010; Rodgers & Kitching, 2011; Potapov et al., 2020)

Possible explanations for the lack of relevant studies from temperate deciduous forests would be their absence, or, according to Shaw (2013), relatively thin accumulations of organic material. However, in a recent study on accidental epiphytes in the Harz Mountains in central Europe, Hoeber & Zotz (2021) found that crown microsoils in the crotches of sycamore maple were quite abundant with substantial volumes of organic matter up to 9 L. They occur across the region, in urban and natural areas. This surprising observation was motivation for the current study, in which we provide the first characterization of the associated fauna.

Crotches are a form of container habitat (Kitching, 2000). Since they are patchily distributed and isolated from each other in the landscape, they can be conceptualized as terrestrial island systems (Gillespie & Roderick, 2002) with expected species-area relations (SARs) derived from the theory of island biogeography by MacArthur & Wilson (1969). This pilot study aimed to provide first insights into the structure and ecology of the natural communities of crown microsoil fauna that inhabit tree crotches in Central Europe. Specifically, we investigated crotches of sycamore maple and Norway maple with a focus on meso- and macrofauna.

MATERIAL AND METHODS

Study area

The study was conducted near the city of Clausthal-Zellerfeld in the Harz Mountains in Central Germany (elevation 560 m a.s.l.). In the Region, the bedrock primarily consists of shale, granite, greywacke, and limestone (Anderson, 1975), and the prevalent soil types are podzols and brown earths. Mean annual temperature is c. 6°C and mean annual precipitation is c. 1200 mm, with rainfall being evenly distributed over the course of the year (Glässer, 1994). The vegetation is dominated by *Picea abies* plantations and secondary deciduous forests (Overbeck & Schmidt, 2012).

Data collection

Sampling was carried out on trees at the edge of a forest stand and single large trees at the campus of the university of Clausthal in June 2019. The choice of individual trees of sycamore maple and Norway maple was based on the presence of crotches of varying size. Crotches were selected to obtain samples from varying amount of detritus (0.03 L to 5.00 L). Height above ground varied between 0.80 m and 3.4 m. Each of the twelve crotches was from a different tree.

When completely removing the detritus, we took care to disturb the sample as little as possible in order to not compromise subsequent extraction. Crotches were then filled with water using a measuring cylinder until the level of the original height of the detritus was reached. This volume was taken as the size of the habitat.

The extraction of organisms was done using Tullgren funnels. This method uses an electric bulb that drives the animals downwards via a funnel into a collecting container by drying out the sample (Tullgren, 1918). Two different sizes of the apparatus were built to hold "small" and "big" samples. A light bulb (Philips 400 W), powder funnels (diameter: 10 cm (small), 15 cm (big)), pipe sections (diameter: 7 cm (small), 15 cm (big); length: 14 cm), plastic grids with a mesh size of 0.5 cm, and beakers with 70% ethanol were used to build the apparatus. Pipe sections were attached to the upper funnel openings to accommodate larger amounts of crown microsoil. The grids were fixed to the lower funnel openings. During extraction, a temperature gradient ranging from 27°C up to 33°C was created whereas temperature was measured at the sample surface. The starting temperature was adjusted according to Sakchoowong & Nomura (2007) and the extraction was considered complete when no more moisture was apparent on the inner surface of the funnels. This took up to 15 days depending on the sample size. The positions of the apparatus were changed daily underneath the electric bulbs so that differences in light intensity could barely influence the outcome of extraction.

Table 1. Occupancy (number of crotches) and total abundance of 14 taxa in 12 crotches of maple trees. Crotch size varied from 0.06 to 5 L and height above ground from 0.8–3.4 m.

Taxon	Occupancy	Abundance
Collembola	11	1660
Coleoptera	10	194
Diptera	10	70
Julida	9	294
Hymenoptera	9	26
Gamasida	8	180
Oribatida	7	531
Isopoda	6	68
Lithobiomorpha	6	42
Thysanoptera	4	7
Araneae	3	8
Enchytraeida	2	63
Crassiclitellata	1	4
Hemiptera	1	1

The crown microsoil fauna was separated by taxonomic orders (Schaefer et al., 2018) and individuals were counted by hand using an Olympus SZX2-ILLB stereo microscope, except for Collembola. Individual collembolans were counted using the image processing methodology of Caridade et al. (2011). Images were made using a Canon EOS 5DSR (DS 126611) digital camera and a HerbScan Light Box (Number 009). Both juveniles and adults were included in the counts. Specimens were preserved in ethanol (70%).

The relationships between taxon abundance and richness with crotch size were analysed by applying linear regression models using R (R Core Team, 2021), considering only soil organisms from the decomposer food web (Swift et al., 1979). A sample in which none of the target taxa were observed was excluded from analyses.

RESULTS

The sample of 12 crotches from sycamore and Norway maples, varying in volume from 0.03 to 5 L, yielded a total of more than 3000 individuals from 14 orders (Table

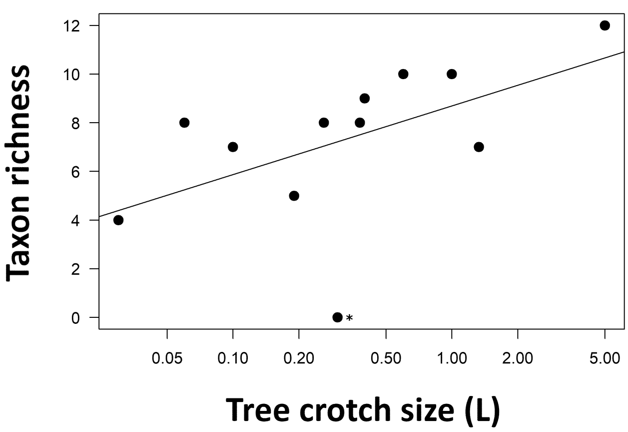

Fig. 1. Relationship between crotch size (volume in L) and taxon richness. Each data point represents one sample. Note the log scale of the x-axis. The solid line represents the linear regression (Taxon richness = 8.53 + 2.06 *log(crotch size), r^2 = 0,4, $p < 0.05$). The empty sample (*) is excluded.

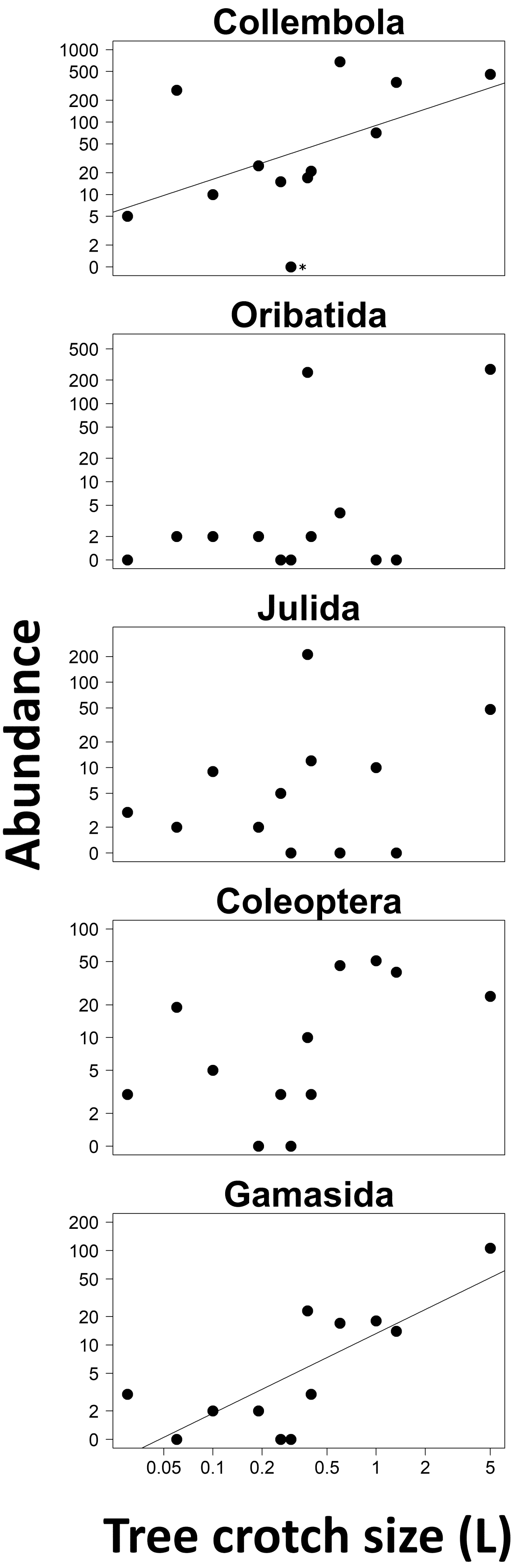

Fig. 2. Relationship between crotch size (volume in L) and abundance in the five most abundant taxa. Each data point represents one sample. Note the log scale of both axes. Solid lines indicate significant linear regressions ($p < 0.05$). The empty sample (*) is excluded.

1). Collembola was by far the most abundant group, accounting for more than 50% of all individuals, and also displayed the highest level of occupancy – collembolans occurred in all but one sample. This relationship between the abundance of taxa and the number of occupied sites was observed for the majority of groups: The second most abundant group with more than 500 individuals, Oribatida, occurred in 7 samples, while 63 individuals of Enchytraeida were found in just two samples.

As expected, there was a positive correlation between taxon richness and crotch size (Fig. 1). The relationship between abundance and crotch size was analysed for individual orders. Only two taxa (Collembola and Gamasida) exhibited the expected increase in abundance (Linear regression, $p < 0.05$, Fig. 2). Apart from a suggestive trend in Coleoptera ($p < 0.1$), variation in abundance was largely independent of habitat size in all other groups (Fig. 2).

DISCUSSION

The tree crotches of sycamore maple and Norway maple trees in the Harz Mountains host a surprisingly rich fauna, comprising all the major elements of the terrestrial soil decomposer food web, such as Collembola, Diptera, Hymenoptera, Oribatida, Gamasida, Enchytraeida, and Crassiclitellata. We also observed members of groups like Hemiptera and Thysanoptera that are not classified as soil animals (Swift et al., 1979). The soil mesofauna (Collembola, Oribatida and Enchytraida) function as bacterial and fungal population regulators, and the saprophagic species among them additionally consume and decompose large quantities of litter (Hättenschwiler et al., 2005). The macrofauna (Julida, Isopoda and Crassiclitellata) displaces and fragments litter, transforming it into considerable amounts of feces. These processes stimulate microbial activity and facilitate decomposition (Hättenschwiler et al., 2005). Araneae, Gamasida and – with a few exceptions – Lithobiomorpha, are predators (Lavelle & Spain, 2001). Epedaphic Gamasida specialize on Collembola, but life-forms living in soil habitats other than the litter layer have different food preferences, e.g. nematodes (Koehler, 1999). The presence of distinct feeding guilds, e.g. predatory and non-predatory species within groups like Oribatida (Lebrun & van Straalen, 1995) and Collembola (Rusek, 1998), however, does not allow for a detailed classification of the functional diversity of the observed fauna in our study.

The observed communities are clearly allochthonous, i.e. they depend on external resources provided by litter fall and rainfall (Kitching, 2000). Differences in stem flow chemistry can strongly influence population and community dynamics (Carpenter, 1982). The substantial differences in crown microsoil moisture among individual tree crotches after rain events, as reported herein for the Harz Mountains, suggest that the availability of litter and rain water is highly variable at the scale of individual trees (Hoeber & Zotz, 2021). Studies on water-filled tree holes have shown that tree-hole size, the amount of detritus, and the height of the tree hole above ground, are all important drivers of local community structure (Petermann & Gossner, 2022).

In this pilot study on crown microsoil crotches, we did not control for height above ground when choosing crotches and the sample size is too small to include both variables in the analyses. Our sampling was not spatially explicit either, because the main purpose of this study was to establish that crown microsoils with an associated rich canopy fauna are not restricted to rainforests in the temperate zones (Wardle et al., 2003; Enloe et al., 2006; Armesto et al., 2009), but can be found in regions like the Harz mountains with a moderate annual rainfall of about 1200 mm.

While acknowledging the limitation of our data set, we can still place our data in the larger context of ecological theory. Following an island biogeographical approach, Wardle et al. (2003) showed that the size of epiphytes had a positive effect on the diversity of meso- and macrofauna at the level of taxonomic order, but abundances either increased or decreased. Richardson et al. (2000) found a significant positive relationship of animal abundance and the amount of crown microsoil within and between two tropical phytotelm systems (*Guzmania* and *Heliconia*). Astonishingly, the taxonomic composition of meso- and macrofauna taxa observed in crown microsoils of vascular epiphytes (Nadkarni & Longino, 1990; Wardle et al., 2003) was similar to that found in this study, revealing a broad similarity of community composition across phytotelm systems among Neotropical cloud forests, warm-temperate rainforests, and tree crotch systems in the temperate zone of Central Europe.

The question of to what extent the height of the crotch above ground affects community structure in our system remains unclear. A few meters between habitable patches (forest floor vs. crotch) may already act as an isolating barrier for many wingless and specialized organisms (Gillespie & Roderick, 2002). However, Bengtsson et al. (1994) showed that there are highly dispersive Collembola that can move from one patch to another. Dispersal into TreMs, such as crown microsoils in crotches, could potentially originate from litter habitats on the ground, as observed for *Entomobrya nivalis* (Meier & Zettel, 1997), or tree trunks, where species like *Orchesella cincta* can be abundant (Prinzing, 2001). Their ability to actively track changes in microclimatic conditions (Prinzing, 2001) make collembolans good colonizers and may explain the high occupancy in the crotches of our study. Oribatida was the second most common group in our study. In comparison to Collembola, their sensory and metabolic capabilities are limited. Responses to different microclimates on bark are slow and non-directional (Prinzing, 2001), but dispersal rates can be higher (Ojala & Huhta, 2001). Aboveground-dwelling species that can be found on trees are *Carabodes labyrinthicus, Cymbaeremaeus cymba, Diapterobates humeralis* and *Phauloppia lucorum*. Specimens collected from Malaise traps (Cordes et al., 2022) suggest that crown microsoils in crotches could be colonized actively, but the main pathway in the colonization of arboreal habitats for Oribatida is wind (Lehmitz et al., 2011). However, both the diversity and abundance of Oribatida living on the bark of *Acer pseudoplatanus* – one of the foundation tree species in our study – can be clearly higher than for Collembola (Nicolai, 1986) and a considerable proportion of Oribatida may have been passively transported into the crotches. Rain has been shown to flush up to 40 individuals per liter down *Carpinus betulus* stems (Ptatscheck et al., 2018). This suggests that colonization of crown microsoils in crotches by Oribatida is mainly a passive, random process driven by wind and rain water.

In contrast, members of the macrofauna often move actively (e.g. Schlägel et al., 2020). Crassiclitellates, for example, can actively reach crotches in a few hours (Eijsackers, 2011). Among the epigeous species that are able to “climb” trees, *Lumbricus eiseni* was found on living individuals in high abundances (Römbke et al., 2012).

Specific abundances are highly variable in time. For example, the majority of euedaphic and hemiedaphic Collembola can reproduce throughout the year. A female can lay between 100–600 eggs, and the development of larvae takes 40–400 days. Thus, the number of individuals can be highly variable in time (Lavelle & Spain, 2001), which could explain the substantial scatter in our data and the lack of a relationship between abundance and crotch size in the majority of taxa. Compared to microhabitats on the ground, crown microsoil arthropods might exhibit different abundance patterns. Lindo & Winchester (2005) found that collembolans were significantly less common in the high canopy (c. 35 m) than on the forest floor, whereas abundances of Oribatida did not differ.

CONCLUSIONS

Substantial accumulations of organic material can occur in the crowns of broadleaved deciduous trees like sycamore maple or Norway maple in central Europe. Such crown microsoil has rarely been given attention in central Europe and if it has, always in a botanical context (Kiebacher et al., 2018; Hoeber & Zotz, 2021). Water-filled tree holes in turn have been the focus of a number of studies in the past decade (e.g. Petermann et al., 2016; Gossner, 2018; Gossner & Petermann, 2022). We conclude that crown microsoils in crotches lend themselves as a natural laboratory with which to study many aspects of community assembly, similarly to water-filled tree holes:

Crown microsoils in the crotches of sycamore maple occur commonly across the landscape of the Harz Mountains region and are frequently occupied by members of the terrestrial soil decomposer food web. These TreMs are distinct units, isolated from each other with substantial variation in size and height above ground. Such features allow them to be conceptualized as terrestrial island systems where fundamental ecological theories e.g. Mac Arthur and Wilson’s theory of island biogeography (1967), and related patterns like SARs, can be studied. Most crotches can be accessed using a ladder, and furthermore the structural simplicity of crown microsoils allows *in situ* manipulations. Experiments that relate to processes such as community (re)-assembly can therefore be carried out in the field at manageable temporal and spatial scales. Observational and experimental studies are now underway with the aim of uncovering the regional diversity of meso- and macrofauna and to obtain information on the ecological importance of crown microsoils in crotches. The major questions are (1) How do crown microsoils in crotches develop over time? (2) Which parameters and processes shape mesofauna community structure in this TreM? (3) Are arboreal communities in crotches different from communities in co-occurring terrestrial microhabitats?

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