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Tree hollow parameters and their effects on saproxylic arthropod diversity: A multi-taxon approach

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Abstract

1. Tree hollows are keystone structures for biodiversity in forest ecosystems, promoting diverse saproxylic communities. However, intensive forest management in central Europe has made them rare. Consequently, saproxylic arthropods inhabiting tree hollows are among the most endangered invertebrates. Most studies on arthropod diversity in tree hollows have focused on beetles.
2. To understand this complex habitat, non-beetle arthropod groups and their habitat requirements must also be investigated. We collected arthropods emerging from 40 tree hollows in beech trees in 2014 and a subset of 23 in 2015 in a managed forest in southern Germany using emergence traps. DNA metabarcoding identified non-beetle arthropods, assessing the influence of tree hollow parameters and forest structure on α- and β-diversity of the most species-rich taxa.
3. Parameters influencing α- and β-diversity differed by year and taxa. The most important factors positively affecting α-diversity were tree hollow volume, tree circumference and entrance area/lateral surface, while entrance area and decomposition negatively affected α-diversity. Beta-diversity was influenced by tree circumference, tree hollow volume, entrance area and forest structure (dipterans: dead wood amount, spiders: nearby tree hollows).
4. These results highlight the importance of heterogeneous tree hollows and forest structures, emphasising the need for their conservation to support highly diverse saproxylic communities.

KEYWORDS
arachnids, collembola, hymenoptera, lepidoptera, metabarcoding, Saproxylic diptera, temperate forest

INTRODUCTION

Dead wood and dying trees are key habitats in forests promoting the diversity of facultatively or obligately dead wood dependent species (Müller et al., 2020; Seibold et al. 2016a; Stokland & Siitonen, 2012; Ulyshen, 2018). Approximately 20%–25% of forest species in central European forests are assumed to be saproxylic (facultative and obligate) (Siitonen, 2001), and thus depend on dead or dying wood, wood-inhabiting fungi, or the presence of other saproxylic species in at least one stage of their life cycle (Speight 1989; Stokland &

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Siitonen, 2012). For beetles, the percentage of saproxylic species is even higher, with 28% of obligate and 19% of facultative species (Graf et al., 2022).

Over 95% of forests in Europe are managed forests (Morales-Hidalgo et al., 2015) that are often homogenous in terms of tree species composition and age structure (Paillet et al., 2010; Smolis et al., 2023). Forest management practices also have a high impact on the amount of dead wood and the abundance and diversity of tree microhabitats such as tree hollows (Paillet et al., 2010; Siitonen, 2001). Tree hollows are dead wood structures in living trees, forming a long-lasting habitat that is characterised by stable abiotic conditions (pH, temperature, humidity) (Henneberg et al., 2021; Lindman et al., 2023; Micó, 2018; Schauer et al., 2018). As the biotic and abiotic configuration of each tree hollow is considered unique and highly complex (Gouix & Brustel, 2012; Micó et al. 2015; Schauer et al., 2018; Henneberg et al., 2021), tree hollows harbour functionally and taxonomically more diverse communities than any other dead wood habitat and are, therefore, regarded as keystone structures for biodiversity in forest ecosystems (Müller et al., 2014). However, in Central European managed forests, tree hollows have become rare structures over the last decades due to intensive forest management, which led to a decrease in numbers of veteran deciduous trees (Lindenmayer et al., 2012). Hence, saproxylic arthropods inhabiting tree hollows are one of the most endangered invertebrate groups due to the severe loss of habitat (Lindman et al., 2023; Micó, 2018; Seibold et al., 2015; Ulyshen, 2018).

Dead wood contains both facultative saproxylic species, using and benefiting from different dead wood structures but not requiring them, as well as obligate saproxylic species that strictly require dead wood structures (Speight 1989, Lofroth, 1998, Siitonen & Ranius, 2015). For tree hollows especially, there are additionally two levels of habitat specialisation: tree hollow generalists that use tree hollows but also other deadwood structures and tree hollow specialists that are strictly dependent on tree hollows. These tree hollow specialists obligatorily complete most of their life cycle in tree hollows and represent an exceptionally threatened group. Of the order Coleoptera, approximately 86% of specialist species in tree hollows in Germany are considered to be threatened or endangered (Floren & Schmidl, 2008). However, not much is known about the community composition of non-beetle arthropod groups living in tree hollows, as most studies on tree hollow-dwelling saproxylic arthropods have been conducted with beetles.

For beetle communities in tree hollows it has been shown that their diversity is influenced by certain characteristics of tree hollows (Henneberg et al., 2021; Micó, 2018; Quinto et al., 2014; Ranius et al., 2024; Schauer et al., 2018). Ranius et al. (2024) recently conducted a review demonstrating that tree diameter, the height of the tree hollow relative to the ground, and the size and orientation of the entrance are the primary factors influencing invertebrate species richness in tree hollows. Other characteristics, including tree hollow volume (Henneberg et al., 2021; Quinto et al., 2014; Schauer et al., 2018), the decomposition stage of wood mould (Henneberg et al., 2021; Schauer et al., 2018; Sverdrup-Thygeson et al., 2010), and additional structural and ecological factors, also play significant roles in shaping species richness within tree hollows (for a comprehensive overview, see Ranius et al. (2024)).

In addition to the characteristics of tree hollows themselves, the amount of dead wood in the surrounding forest area seems to positively influence saproxylic beetle α-diversity in tree hollows if the tree species composition in the respective forest stand contains a high proportion of deciduous tree species (Henneberg et al., 2021). However, not much is known about the characteristics of tree hollows or the parameters of forest structure that influence the diversity of non-beetle arthropod groups inhabiting tree hollows.

Compared with saproxylic beetles, the ecology of saproxylic Diptera remains poorly studied (Ulyshen, 2018). Unlike most beetles, saproxylic flies are assumed to prefer moist to wet microhabitats and typically dominate insect assemblages in water-filled tree hollows (dendrotelms) (Blakely et al., 2012; Majumder et al., 2011; Siitonen, 2012; Srivastava & Lawton, 1998; Yanovlak, 2001). Although some saproxylic fly species are opportunists that utilise a wide range of wet dead wood structures, many of them are restricted to tree hollows (Blakely et al., 2012). Hoverflies represent the most well-studied family of saproxylic flies (Ricarte et al., 2009; Ulyshen, 2018).

The habitat requirements of saproxylic hymenopterans (bees and wasps) also remain poorly studied (Bogusch & Horák, 2018). While dead wood is a very important nesting habitat for aculeate hymenopterans, only a few species can excavate their own cavities in wood (Bogusch & Horák, 2018). An estimated 21% of the central European aculeate hymenopteran species nest in various cavities, and 30% of these are assumed to highly prefer tree hollows (Bogusch & Horák, 2018). Therefore, an important factor for the survival of saproxylic bees and wasps in forests is the retention of standing dead wood (Westerfelt et al., 2015) and the conservation of hollow-bearing trees, which has been confirmed by findings from other regions including the tropics (Thiele, 2005). It is surprising that this fauna has received so little attention, particularly given the huge importance of pollinators, including the European honeybee, *Apis mellifera* L., which is itself saproxylic (Bogusch & Horák, 2018). Before domestication, the European honeybee was nesting almost exclusively in tree hollows (Michener, 2007; Nieto et al., 2014). Bumblebees usually nest in the ground but will sometimes also nest in cavities above ground, including tree hollows (Goulson, 2003).

An aspect that often receives less attention in biodiversity research is β-diversity (Isbell et al., 2018; Müller et al., 2023; Schauer et al., 2023). It is a measure of dissimilarity in species assemblage composition in space or time and has been seen as determined mainly by environmental differences among locations; the more similar the environment, the more similar the fauna (Whittaker, 1960). However, an increase in similarity in species composition between sites (biotic homogenization) can have severe ecological and evolutionary consequences when local (α-) and regional (γ-)diversity decrease and taxonomic distinctions among regions vanish (Gossner et al., 2016; Olden et al., 2004; Rolls et al., 2023). Thus, understanding the drivers of changes in β-diversity is crucial to enable environmental managers and conservation practitioners to make informed decisions about

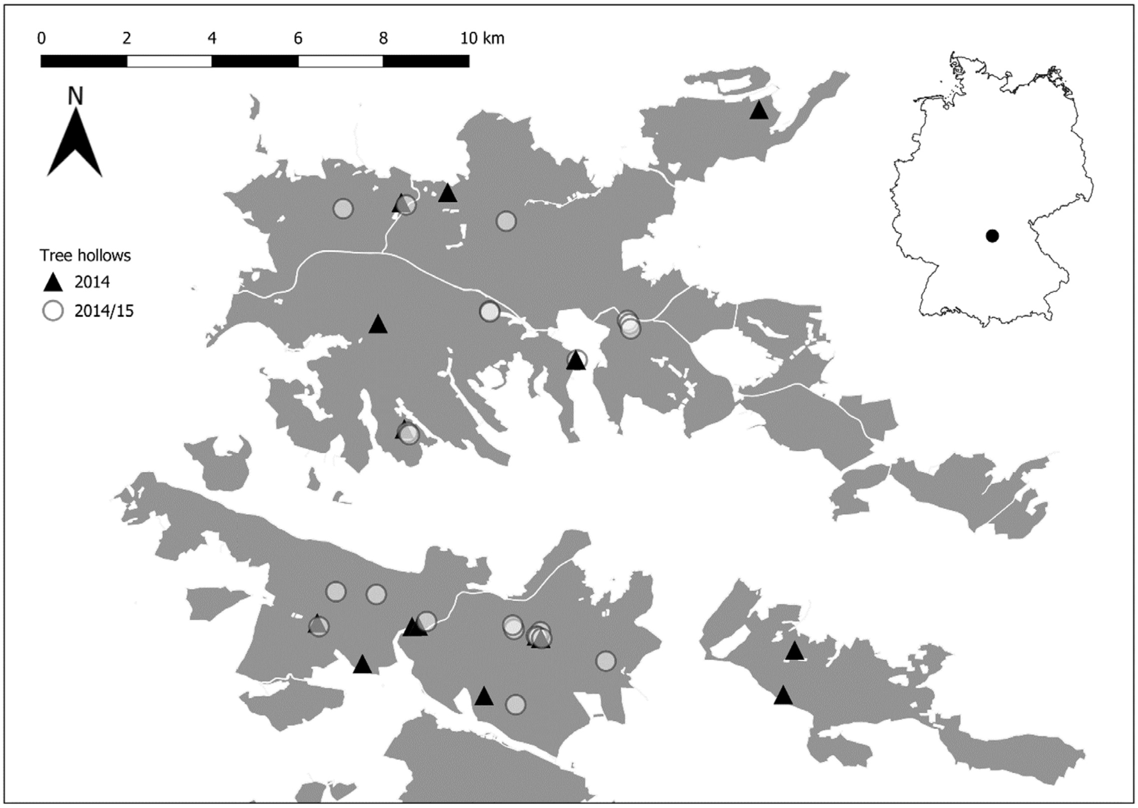

FIGURE 1 Location of all 40 sampled tree hollows in the forestry department of Ebrach (Bavaria, Germany). Triangles represent tree hollows sampled in 2014 and circles represent tree hollows sampled in 2014 and 2015. Grey area indicates part of the forest district of Ebrach.

which interventions may be required to sustain regional diversity (Rolls et al., 2023; Schauer et al., 2023).

In recent years, DNA metabarcoding, the coupling of DNA barcoding with high-throughput sequencing, enabled time- and cost-effective assessments of biodiversity by allowing the analysis of bulk samples of specimens (Ji et al., 2013; Taberlet et al., 2012; Yu et al., 2012). This is urgently needed because high abundances of small arthropods combined with cryptic morphology, lack of taxonomic expertise, and sometimes a high incidence of undescribed species pose serious challenges to their identification (Bickford et al., 2007; Young & Hebert 2022; Schauer et al., 2023).

In this study we use DNA metabarcoding to analyse α- and β-diversity of bulk samples of arthropods from tree hollows. We assess the influence of tree hollow characteristics as well as the number of tree hollows in the near surrounding, and dead wood amount in a radius of 100 m around the tree hollows on α- and β-diversity of non-beetle arthropods in the hollows. We aim at answering the following study questions: (1) Do tree hollow characteristics or parameters of forest structure that have been shown to influence the diversity of saproxylic beetles in tree hollows also drive α-diversity of other hollow-dwelling arthropod taxa? (2) Which factors drive β-diversity of non-beetle arthropod assemblages in tree hollows?

We hypothesize that (I) there will be positive relationships between arthropod α-diversity and parameters that describe the area or volume of potentially suitable habitat within a tree hollow, for example, hollow volume or entrance area/lateral surface. (II) Early or intermediate stages of wood mould decomposition will positively influence α-diversity in the hollows analogously to saproxylic beetles. (III) β-diversity will be driven by highly contrasting environmental parameters, that is, dissimilarity of arthropod communities will be driven by differences in tree hollow parameters.

MATERIALS AND METHODS

Study area and sampling method

The study was conducted in the years 2014 and 2015 in the northern Steigerwald (Germany, Bavaria). We sampled 40 beech trees with tree hollows in 2014 and a subset of 23 of these with tree hollows again in 2015, with 17 trees not being resampled again due to low saproxylic beetle abundance in 2014 (Figure 1). Only tree hollows with at least 2 cm of wood mould (as a proxy for saproxylic arthropod activity) and a height less than 2 m from the ground (due to safety reasons) were chosen. Entrances of tree hollows were closed with acrylic mesh from mid of March to mid of April to prevent nesting of vertebrates. After that, emergence traps, containing pure ethanol (99.8%), were installed to catch all emerging arthropods in the period from April to August. Traps were emptied biweekly. For more detailed information on sampling, see Schauer et al. (2018).

Characterisation of tree hollows and tree hollow parameters

A characterisation of each tree hollow was based on the following tree hollow parameters (for tree hollow measurements see Table S1):

- Tree circumference at 130 cm height from ground.
- Tree hollow volume: calculated as standardised cylinder with a circular base with the formula $V = \pi^*r^{2*}h$ [cm^3] whereby r is the radius of the hollow itself, measured at the entrance, and h is the total height of the hollow. Height was measured with a measuring tape from the base to the roof of the hollow.
- Height above ground: hollow distance to the ground [cm] from the lowest point of the hollow entrance.
- Tree hollow entrance: size of tree hollow entrance area calculated as an ellipse with the formula $area = \pi^*a^*b$, where a is half the height and b half the width of the ellipse.
- Proportion lateral surface to hollow entrance: calculated with the formula 100 * a/b, where a is the area of hollow entrance and b is the lateral surface (area of an object, excluding the top and bottom area: calculated with the formula $lateral\ surface = a^*b$ [cm2], where a is the height of the tree hollow and b its circumference) of the tree hollow. The ratio of entrance area to lateral surface describes whether it is big tree hollows with small entrance or vice versa.
- Mean annual solar irradiation: calculated based on surface slope, inclination direction, elevation and coordinates (of tree hollows) using Points Solar Radiation tool as part of the Spatial analyst tools for ArcMap 10.3.
- Degree of decomposition: Wood mould was sampled from the base of the hollow. Mould was collected at a depth of 2 cm below the surface of the mould to 7 cm depth. Mould was classified into four stages of decomposition. We used three parameters to determine the stage of decomposition (colour, texture of the detritus and visible woody parts).

  Stage 1: yellow to light brown in colour, visible woody parts of bigger size, low decay.

  Stage 2: light brown to brown in colour, visible woody parts of smaller size, medium decay.

  Stage 3: brown to dark brown in colour, almost no visible woody parts, medium to high decay.

  Stage 4: dark brown to black in colour, no visible woody parts, high decay.
- Surrounding tree hollows: the number of all tree hollows in a radius of 50 m around each sampled tree hollow. Tree hollows were checked for wood mould, if possible in terms of height at the trunk.
- Amount of dead wood in a 100 m radius: Forest inventory data was collected by the Bavarian state forest authorities (BaySF) in 2012 and kindly provided to us. Since forest inventory data was recorded as point data with a sampling point at each node of a 200 m x 200 m grid, it was interpolated to a continuous spatial distribution using the software ArcGIS (ESRI 2018). To obtain values for each sampled tree hollow, we drew circular buffers with a radius of 100 m around each tree hollow and calculated the value of dead wood amount within each buffer using the software ArcGIS (ESRI 2018).

DNA metabarcoding of tree hollow arthropods

Arthropods caught in the emergence traps were identified by DNA metabarcoding using next-generation sequencing. DNA metabarcoding and bioinformatic processing was carried out by the AIM. science—Advanced Identification Methods GmbH (Leipzig, Germany) (for methodological details about DNA metabarcoding process and following computational pipeline see Hausmann et al., 2020). Arthropod sequences were matched against the publicly available DNA barcode library within the Barcode of Life (BOLD—v4.boldsystems.org [Ratnasingham & Hebert, 2007]), NCBI Genbank (Benson et al., 2013) and RDP (Ribosomal Database Project Classifier algorithm -CO1 trained [Porter & Hajibabaei, 2018]). In the following sections, the species numbers of arthropod communities are derived from the Barcode Index Numbers (BINs), a persistent species-level taxonomic registry based on the analysis of patterns of sequence variation in the barcode region for the delineation of species (Ratnasingham & Hebert, 2013). For a more balanced and independent identification of existing classifications (Hausmann et al., 2013) we used BINs as a surrogate of species richness, as they are more reliable than OTUs. We used a 97%-Hit-%-ID threshold (similarity overlap of OTU sequences of at least 97% with the Barcode of Life sequence databases). For simplification and due to our multi-taxa approach, we refer to species richness and not BIN richness for arthropods. The taxa diptera, hymenoptera, lepidoptera, collembola and araneae were chosen for analysis, as they were present in sufficient abundance and species numbers. Coleoptera caught during the sampling period had been the focus of an earlier study (Schauer et al., 2018) and were therefore not included in the present analysis.

Data analysis

All statistical analyses were carried out in R version 4.0.2 (R Core Team, 2021). Prior to statistical analysis, species emerging from the same tree hollow that was sampled biweekly over the whole sampling period were pooled. We analysed three different data sets separately: (1) species sampled in 2014 (40 tree hollows in total), (2) species sampled in 2015 (23 tree hollows in total) and (3) species emerging from the same tree hollow in 2014 and 2015 pooled (23 tree hollows in total). We analysed three data sets from the different years to account for temporal changes between the sampling years. Here we present the data for the pooled dataset, as this dataset covers the species diversity of both years by collecting species recolonising the tree hollow and species that have a longer development time. Results of the dataset from 2014 and 2015 can be found in the supplement. We analysed α-diversity using generalised linear models (GLM) for Poisson-distributed data (Bolker et al., 2009) by comparing the mean

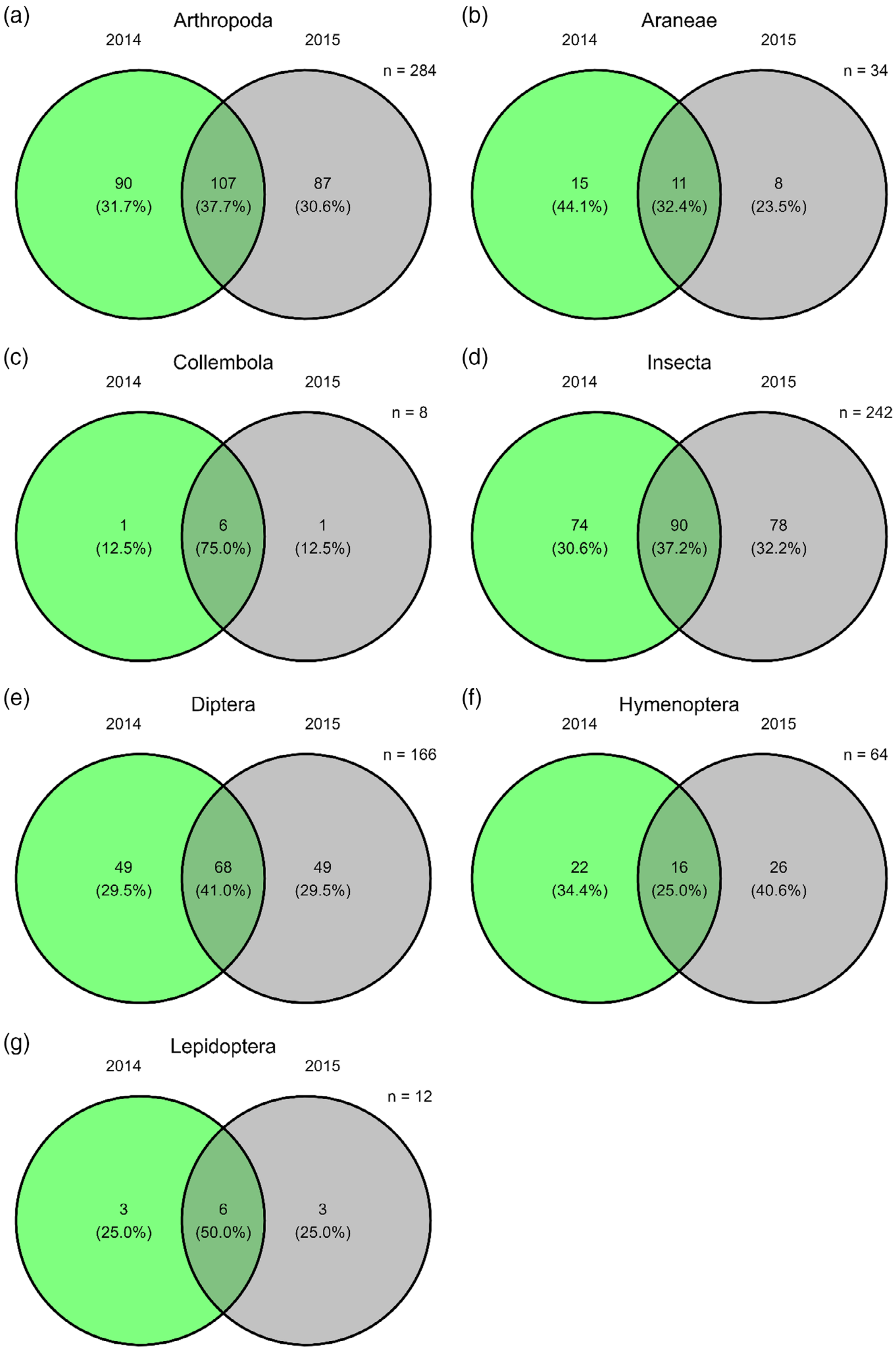

FIGURE 2 Species numbers of arthropods sampled from emergence traps of 40 tree hollows in beech trees in 2014 and 23 tree hollows in 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera.

number of species per tree hollow. Prior to modelling, we calculated the variance inflation factor using the "vif" function with a threshold of 0.5 from the "usdm" package (Naimi et al., 2014). None of the parameters had to be removed due to collinearity issues. We included tree circumference as a predictor and height of the tree hollow from ground, tree hollow volume, size of tree hollow entrance, ratio of entrance area to lateral surface, degree of decomposition of the wood mould, solar radiation, surrounding tree hollows and the amount of dead wood in a 100 m radius as covariates to control for possible confounding variables. Variables were either log- or square-root-transformed to reduce skewness if necessary.

To analyse the effects of the predictor variable and the selected covariates on differences in species community composition among tree hollows (β-diversity), we used the "adonis" function, a permutational multivariate analysis of variance (Legendre & Anderson, 1999), provided by the 'vegan' package (Oksanen et al., 2016). Bray-Curtis distances and 100,000 permutations for the calculation were used to derive the associated resemblance matrices. The predictor variable and covariates were the same as for α-diversity models.

To test if the species richness of beetles in tree hollows can be used as a surrogate for the diversity of arthropods in tree hollows, we tested the species richness of beetles, originating from the same sampling event, against the number of species of all taxa investigated in this study. Therefore, we used the Pearson correlation in the r package "Hmisc" (Harrell Jr., 2024) for the pooled data set of 23 tree hollows sampled in 2014 and 2015.

RESULTS

Species richness and effects of tree hollow characteristics and parameters of forest structure on α-diversity

In total, DNA metabarcoding revealed (a) 284 arthropod species/BINs (90 species unique in 2014, 87 unique in 2015), comprising (b) 34 species of Araneae (15 species unique in 2014, 8 unique in 2015), (c) 8 species of Collembola (1 species unique in 2014, 1 unique in 2015), (d) 243 species of insects (74 species unique in 2014, 78 unique in 2015) and therein (e) 166 species of Diptera (73 species unique in 2014, 78 unique in 2015), (f) 64 species of Hymenoptera (22 species unique in 2014, 26 unique in 2015), and (g) 12 species of Lepidoptera (3 species unique in 2014, 3 unique in 2015) (see Figure 2, for the detailed BIN list see Table S2).

None of the tested taxa showed a significant correlation between their species richness and the number of beetle species ($p > 0.05$, Table S5).

For the pooled dataset of 23 tree hollows sampled in 2014 and 2015 arthropod metabarcoding revealed 230 arthropod species/BINs, comprising 25 species of Araneae, 8 species of Collembola, 137 species of Diptera, 51 species of Hymenoptera and 9 species of Lepidoptera. Species numbers increased significantly with larger tree hollow volume and higher ratio of entrance area and lateral surface. Larger entrance area and a higher degree of decomposition of the wood mould led to significantly fewer arthropod species. This pattern was mainly driven by insects, especially Diptera. Additionally, for insects higher solar radiation correlated with a higher species number. For Hymenoptera species numbers decreased significantly with increasing height from the ground of tree hollows. For Araneae, Collembola, and Lepidoptera no significant effects were found (see Figure 3 and Table S3).

Effects of tree hollow characteristics and parameters of forest structure on β-diversity

The β-diversity of arthropod communities collected from different tree hollows (pooled from 2014 and 2015) was driven by the differences in tree circumferences, especially for insects and therein Diptera and Hymenoptera. This means that communities sampled from trees that differed more in circumference harboured arthropod communities that differed more from each other. Also, the volume of tree hollows had a significant influence on the change of insect communities. β-diversity of Araneae, Collembola and Lepidoptera was not affected by any of the tree hollow parameters in this study (see Figure 4 and Table S4).

DISCUSSION

The findings of this study show that different hollow-dwelling saproxylic taxa have distinct habitat requirements regarding characteristics of the tree hollow. We highlighted the drivers, especially of the large group of saproxylic dipterans living in tree hollows, for the first time. Dipteran species richness increased with hollow volume and tree circumference but was negatively affected by the degree of decomposition and the area of the hollow entrance. While the effects of the former three parameters were found to be similar for beetle species richness in tree hollows, the negative effect of a larger entrance area on Diptera contrasts with the results found for beetles, whose assemblages were more species rich in hollows with larger entrances (Quinto et al., 2014).

Most of the species in this study might not meet the strict definition of Speight (1989) being saproxylic as they require deadwood at some point of their lifecycle (obligate saproxylic). It might be that some of the species are generalistic and just occasionally visit tree hollows. However, according to Lofroth (1998) there are also facultative saproxylic species that may use dead wood but do not require it. They clearly benefit from dead wood as a resource, for example, as hunting ground or for nesting (Stokland & Siitonen, 2012). Additionally, for a lot of species, it is not known if they are obligate or facultative saproxylic. Therefore, we use the term saproxylic for the species identified in our study.

α-Diversity

The results of this study show that α-diversity of non-beetle arthropod taxa in tree hollows is related to different tree hollow characteristics. In contrast, parameters of surrounding forest structure like the number of surrounding tree hollows and the amount of dead wood had no significant effects on α-diversity of any of the taxa in this study.

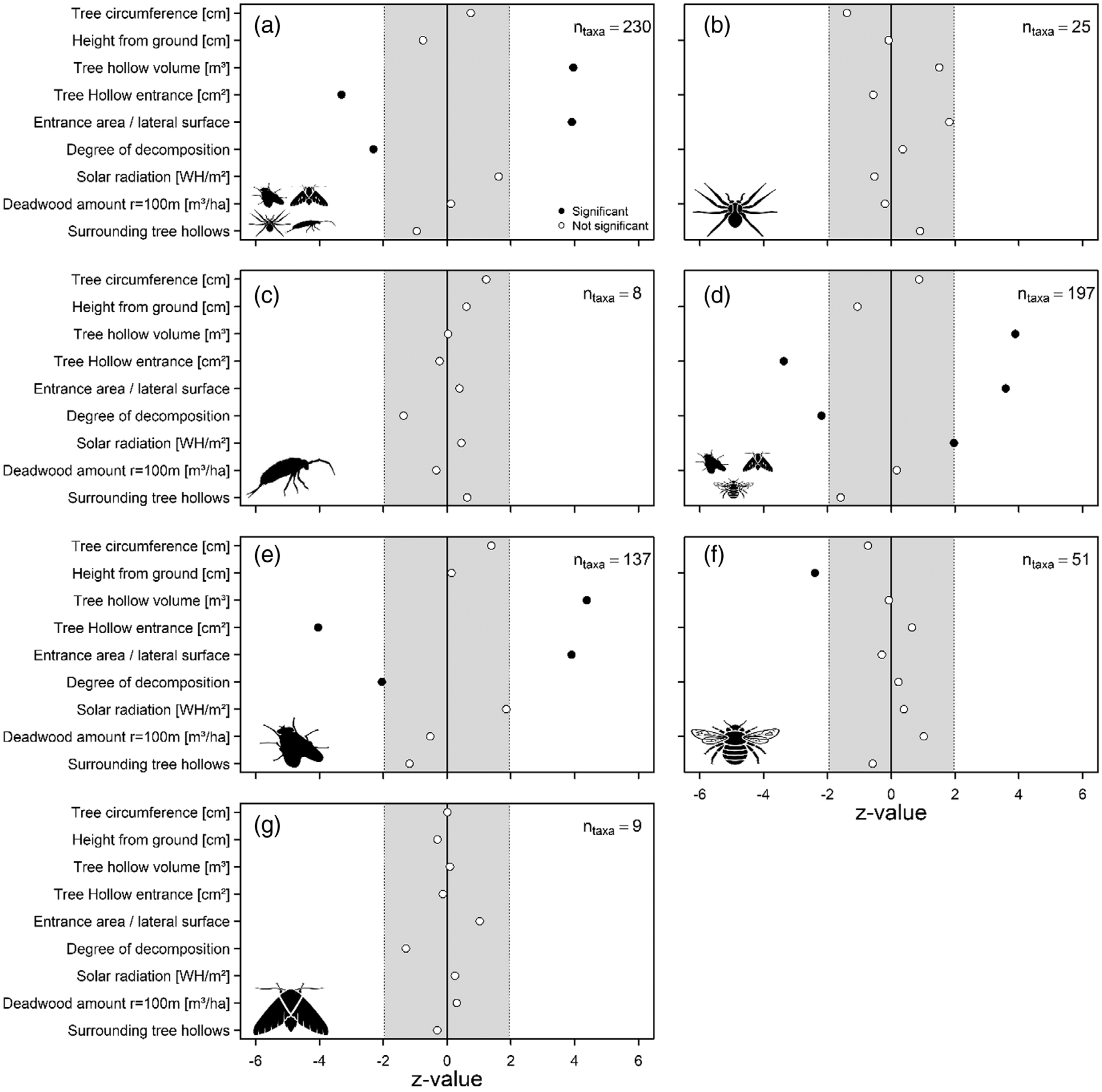

FIGURE 3 α-diversity of arthropod samples collected with emergence traps of a subset of 23 tree hollows in beech trees pooled from 2014 and 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera. Grey area represents significance borders ($p < 0.05$), white dots = non-significant effects; black dots = significant effects; n_{taxa} = number of species.

The largest proportion of taxa included in this study were insects (242 of 284 taxa), and within insects, the largest proportion was comprised of Diptera (166 taxa), followed by Hymenoptera (64 taxa). In a former study conducted with the same methods and at the same time, we reported 89 species of saproxylic beetles (Schauer et al., 2018). Contrary to the literature (Siitonen, 2012) the most species-rich taxon in our study was Diptera and not Coleoptera. There is a low probability that these differences compared with the literature originate from the different identification methods. However, Salis et al. (2024) showed a high consistency in identified species between barcoding and classic identification by taxonomists. In accordance with our findings, Ulyshen (2018) proposed Diptera to be the most diverse saproxylic taxon, with saproxylic habits known by at least 75 (48%) of the 157 fly families recognised globally. The effects of tree hollow parameters on α-diversity of Insecta and Arthropoda were mainly driven by Dipterans. This is corroborated by the fact that α-diversity of the two non-insect taxa, Araneae and Collembola, showed no significant relation with any of the tree hollow parameters. However, Araneae are an important species group in tree hollows. Hernández-Corral et al. (2021) found 87 species, including endemic and vulnerable species in oaks in Spain. They found a positive relation of spider species richness with tree hollow height and beetle richness.

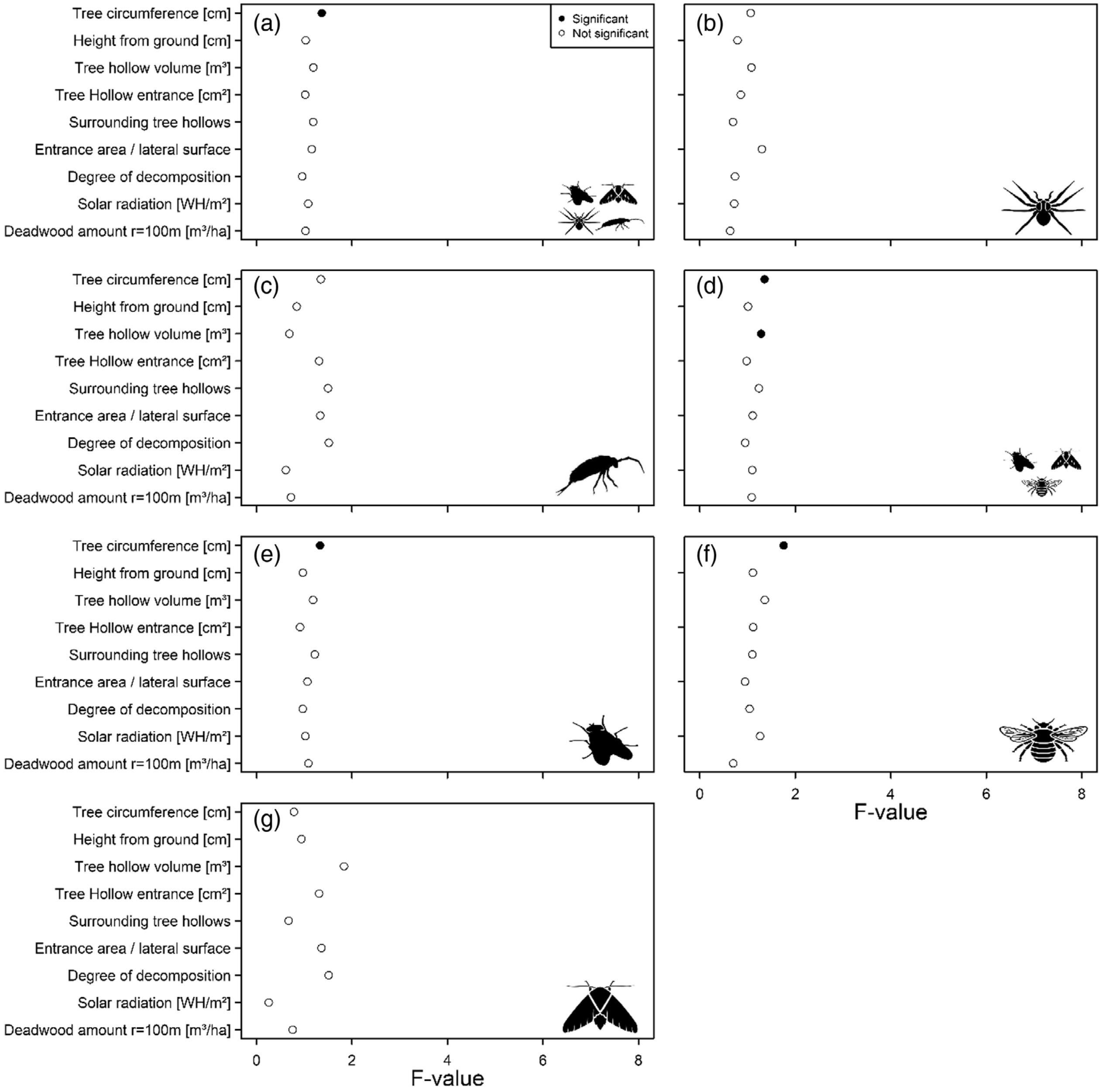

FIGURE 4 β -diversity of arthropod samples collected with emergence traps of a subset of 23 tree hollows in beech trees pooled from 2014 and 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera. Grey area represents significance borders ($p < 0.05$), white dots = non-significant effects; black dots = significant effects; n_{taxa} = number of species.

Tree hollow volume, a characteristic that is one of the most important characteristics for the species richness of other taxonomic groups like beetles, did not affect species richness in spiders but abundance.

The strongest significant relation between tree hollow parameters and α-diversity was the same for the higher-level taxa Insecta and Arthropoda, mainly driven by Diptera: positive effects of tree hollow volume, tree circumference, and entrance area/lateral surface, and negative effects of tree hollow entrance area and degree of decomposition. The positive effects of the area or volume of potentially suitable habitat within a tree hollow on arthropod α-diversity (hypothesis I) may be driven by the potentially higher number of different microhabitats within the hollows (Habitat Heterogeneity Hypothesis, HHH). The HHH explains species diversity as a function of habitat diversity (MacArthur & MacArthur, 1961; Seibold, Bässler, Brandl, et al., 2016; Tews et al., 2004). Different microhabitats can support many specialised arthropod species with specific habitat requirements. Thus, habitat heterogeneity allows coexistence by reducing competition (Darío Hernandes Córdoba et al., 2024; Siitonen, 2012). Tree hollow volume has been shown to influence α-diversity of hollow-dwelling saproxylic beetles and hoverflies (Diptera: Syrphidae) (Henneberg et al., 2021; Quinto et al., 2014; Ranius et al., 2024; Sánchez-Galván et al., 2014; Schauer et al., 2018). Quinto et al. (2014) reported that guild richness of saproxylic beetles and hoverflies in tree hollows in Iberian Mediterranean woodlands was positively related to tree hollow volume. Similarly, Sánchez-Galván et al. (2014) found that, in addition to water content and presence of cetoniid beetle larvae, height and size of tree hollows were important determinants of hollow-dwelling syrphid assemblages in Spain. The positive effect of tree circumference on α-diversity of dipterans and the two higher-level taxa (arthropods and insects) in 2015 in this study could be interpreted in the same vein: large-diameter trees often contain larger hollows than small-diameter trees (Jonsell, 2004), and therefore offer a larger volume of potentially suitable habitat and a greater diversity of microhabitats for hollow-dwelling dipterans.

Tree hollow entrance area showed a negative effect on α-diversity of dipterans (and thus higher-level taxa arthropods and insects). Since tree hollows with upwards facing entrances are associated with higher humidity and less evaporation (Lindman et al., 2023), this finding might be consistent with the fact that saproxylic dipterans depend on wet or even water-saturated substrates (Ulyshen, 2018). It has been reported that saproxylic flies often dominate arthropod assemblages in saturated or submerged dead wood (Braccia & Batzer, 2008; Hövemeyer & Schauermann, 2003). Larvae of some families of dipterans are known to dominate insect assemblages in the wettest tree hollows (dendrotelms) (Blakely et al., 2012; Kitching, 1971; Siitonen, 2012), and species of the dominating families Culicidae, Syrphidae, Chironomidae and Ceratopogonidae (Kitching, 2000; Schmidl et al., 2008) were also present in this study (see Table S2). Although only a small proportion of hoverfly (Syrphidae) species are assumed to be saproxylic (approx. 14% of European species), this includes most members of the largest subfamily, Eristalinae (Reemer, 2005; Ulyshen, 2018). Certain hoverfly species have been reported to be dependent on the distinct physical conditions found in wet tree hollows as well as interactions with hollow-dwelling bacteria that have been found in the guts of hoverfly larvae (Sánchez-Galván et al., 2014). Similarly, Blakely et al. (2012) reported that only some of the fly species they found in wet tree hollows in New Zealand were opportunists that utilised a wide range of water bodies, while many of them were restricted to these structures. As tree hollows are characterised by stable physical conditions (Lindman et al., 2023; Micó, 2018; Siitonen, 2012), wet tree hollows might keep their high level of moisture more constantly than other dead wood structures, and especially those hollows with a small entrance area. In contrast to the negative effect of entrance area on species richness of Diptera, we found a positive relationship between beetle diversity and entrance area of the tree hollows (Schauer et al., 2018).

In our study, α-diversity of Diptera, as well as the higher-level taxa Insecta and Arthropoda, was negatively affected by the degree of decomposition of the wood mould. Also, except for spiders (Araneae), all single taxa tended to show a negative relation between degree of decomposition and α-diversity. Therefore, later stages of wood mould decomposition were associated with a lower α-diversity of saproxylic arthropods in tree hollows (hypothesis II). Likewise, early and intermediate stages of wood mould decomposition are associated with higher α-diversity of saproxylic beetles in tree hollows (Henneberg et al., 2021; Schauer et al., 2018; Sverdrup-Thygeson et al., 2010). The nutritional properties of highly decomposed wood mould might not support a broad community of arthropods anymore, resulting in a decline of species richness at later decomposition stages (Stokland & Siitonen, 2012). However, preferences for earlier or later stages of wood decomposition in dipterans seem to depend on feeding guild: while predatory fly taxa are more abundant in earlier stages of decomposition, saprophagous and fungivorous taxa are generally more abundant in later stages of decomposition (Hövemeyer & Schauermann, 2003; Vanderwel et al., 2006). Vanderwel et al. (2006) stated that the higher abundance of predatory flies in earlier stages of wood decomposition probably reflects the higher abundance of phloem- and wood-feeding beetle prey in younger dead wood logs. Syrphids are the best studied Dipterans in tree hollows. In addition to water content, Sánchez-Galván et al. (2014) showed that the presence of cetoniid beetle larvae (positive influence), volume of the tree hollows (positive influence), and height above ground of the tree hollows (positive influence) were also important determinants of hollow-dwelling syrphid assemblages in Spain.

The α-diversity of hymenopterans decreased significantly with the height from the ground of the tree hollow. Likewise, studies on saproxylic beetles have shown that tree hollows that are closer to the ground, and especially tree hollows with connection to the forest floor, are more species-rich than hollows that are located higher up on the tree trunk (Henneberg et al., 2021; Quinto et al., 2014; Ranius et al., 2024; Schauer et al., 2018). It has been proposed that hollows that are closer to the forest floor can be accessed by predatory beetles that crawl on the forest floor, for example, Carabidae or Staphylinidae, which might account for the higher species richness in these hollows (Ranius, 2002; Schauer et al., 2018). However, Ranius et al., 2024 showed that the height of the tree hollow relative to the ground had also negative effects on species richness, depending on the species and study.

This could also account for the higher α-diversity of hymenopterans in this study, as parasitoid hymenopterans, mainly from the families Ichneumonidae and Braconidae (Hilszczański, 2018), can be found in higher diversity when the diversity of potential host insects is higher. The term "saproxylic" with regard to parasitoids means that these species are exclusively or almost exclusively associated with host insects of typical saproxylic families such as wood boring beetles (Cerambycidae, Buprestidae, Ipinae, Anobiidae) or wood wasps (Siricidae, Xiphydriidae) (Hilszczański, 2018). An important ecosystem service provided by saproxylic hymenopteran parasitoids is a top-down reduction of host populations (Berisford, 2011; Wermelinger, 2004). In contrast, saproxylic aculeate hymenopteran species have been shown to prefer cavities higher up on the tree trunk in sun-exposed dead trees (Sobek et al., 2009; Thiele, 2005; Westerfelt et al., 2015).

Parameters of surrounding forest structure, namely the number of surrounding tree hollows and the amount of dead wood, that have been shown to influence α-diversity of saproxylic beetles in the same tree hollows (Henneberg et al., 2021; Schauer et al., 2018) showed no significant effect on α-diversity of any of the taxa examined in this study. Therefore, these taxa might contain a larger proportion of tree-hollow specialist species compared with saproxylic beetles for whom the amount of dead wood amount in general, in the surrounding forest area plays a less important role in their ecology. Also, the opposite might be true, with the species investigated here being even more generalistic than saproxylic beetles, and their diversity may be driven by other habitat characteristics rather than the amount of dead wood. At small spatial scales (up to 500 m) there appears to be no negative effect of habitat isolation on species richness in tree hollows. However, this changes on larger spatial scales or extremely isolated habitats (see Ranius et al., 2024 and references therein).

Saproxylic beetles are the best investigated taxon in tree hollows and are often used as a surrogate for the diversity of tree hollow arthropods. However, we could not find a correlation between the number of beetle species and the number of species of any other taxa investigated in this study. Our data support no evidence that beetle species richness is a surrogate for overall arthropod species diversity in tree hollows. However, the tree hollows sampled in the second year have been the most species-rich tree hollows in the year before, which might influence the outcome. Nonetheless, a multitaxon approach for effective conservation measures for tree hollow communities is of high importance.

β-Diversity

Tree hollow parameters and parameters of forest structure had a significant influence on β-diversity of each taxonomic group in this study except for Lepidoptera. Tree hollows of different sizes did not only differ in α-diversity, but also the dissimilarity of species assemblages increased significantly when tree circumference and hollow volume differed more strongly. Therefore, small-diameter trees and small tree hollows in this study did not just contain a subset of species from larger trees and larger hollows but a different assemblage of species.

Other tree hollow parameters that influenced β-diversity were the size of the hollow entrance and entrance area/lateral surface. Differently sized entrance areas might influence the microclimate in tree hollows and thus lead to communities that either prefer wet or dry conditions. Both preferences are described for dipteran dominated communities, albeit for different groups of Diptera (Kitching, 2000; Schmidl et al., 2008; Ulyshen, 2018).

In contrast to α-diversity, there were effects of forest structure on β-diversity, namely the number of tree hollows in the near surroundings and the amount of dead wood in a 100 m radius. This shows that not only characteristics of the tree hollows themselves influence the dissimilarity of species assemblages in the hollows, but also parameters of the surrounding forest structure, for example, species assemblages in tree hollows in areas with high amounts of dead wood in the surroundings may contain more generalist saproxylic species that can utilise different kinds of dead wood due to a larger local species pool than assemblages in tree hollows with very little dead wood in the surroundings.

Our results show that differences in tree hollow characteristics and surrounding forest structure contribute to species dissimilarity of arthropod communities within the tree. This implicates that a high heterogeneity of differently shaped tree hollows helps to increase overall β-diversity of saproxylic arthropods on a regional scale (Seibold, Bässler, Baldrian, et al., 2016). High β-diversity is important to prevent biotic homogenisation and to increase functionality and resilience against disturbances (Gámez-Virués et al., 2015; Gossner et al., 2016).

Conclusion

To apply effective conservation measures for tree hollow communities, it is crucial to take several taxonomic groups into account and not only focus on the best-investigated group, namely saproxylic beetles. The full range of tree hollows of different sizes and characteristics should therefore be retained, as a broad range of different taxa will benefit from a high heterogeneity of differently shaped tree hollows. Furthermore, management interventions promoting hollow formation should be enforced to conserve the highly diverse saproxylic assemblages living in tree hollows. To provide effective conservation measures, a multitaxon approach should be considered, as the diversity of beetles in tree hollows as a surrogate for overall arthropod diversity is not supported by our results for tree hollow communities.

Moreover, the effects of forest structure on β-diversity imply that the number of tree hollows in the near surroundings of a focal tree hollow as well as the amount of dead wood in a radius of 100 m affects dissimilarity of species assemblages in tree hollows. Therefore, dead wood and dead wood related structures should be taken into consideration by forest managers when developing management programs for hollow-dwelling saproxylic species.

AUTHOR CONTRIBUTIONS

Bastian Schauer: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; formal analysis; data curation. **Benjamin Henneberg:** Writing – review and editing; formal analysis; data curation; visualization; validation. **Elisabeth Obermaier:** Conceptualization; methodology; investigation; supervision; project administration; writing – review and editing; funding acquisition. **Heike Feldhaar:** Conceptualization; methodology; investigation; supervision; funding acquisition; project administration; resources; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of competing interests.

DATA AVAILABILITY STATEMENT

Data can be found on Figshare https://doi.org/10.6084/m9.figshare.28238219.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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