# *Saproxylic arthropods in tree hollows: drivers of diversity at different spatial scales in a regional comparison*

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## Summary

Intensive forest management in past centuries has led to a massive decline of veteran deciduous trees and dead wood structures like tree hollows in central European managed forests. Thus, many species of saproxylic arthropods, which directly or indirectly depend on dead or dying wood or upon the presence of other saproxylics, have become endangered. Tree hollow specialist species that depend on the presence of tree hollows represent an exceptionally threatened group with approx. 75% - 86% of saproxylic beetle species specialized in tree hollows in central Europe being endangered. To effectively conserve the arthropod communities in tree hollows it is important to understand the characteristics of tree hollows, forest structure and surrounding landscape that influence diversity of hollow-dwelling saproxylic arthropods at different spatial scales and how the influence of these factors changes across differently structured forest regions and hollow-dwelling taxa.

In the first manuscript I assessed characteristics of tree hollows, hollow trees and surrounding forest structure that influence the diversity of saproxylic beetles in tree hollows of beech trees at spatial scales of 50 m - 500 m around the focal tree hollows in the three study regions Ebrach, Fichtelberg and Kelheim. In each study region 42 - 50 tree hollows in beech trees were examined using emergence traps over the study period of April to August 2018 and 2019. As a new type of analysis, forest inventory data that are regularly collected by the state forest authorities (BaySF) in all Bavarian state forestries were used. A total of 283 saproxylic beetle species (5880 individuals) were collected, 22% of which were threatened species. The most important local parameters that influenced saproxylic beetle species richness in all three study regions were the entrance area of the hollows (positive influence), the stage of wood mold decomposition (negative) and the height above ground (negative). At radii of 50 m and 100 m around the tree hollows the amount of dead wood positively influenced species richness of hollow-dwelling beetles in the mostly deciduous Ebrach forestry. In the mostly coniferous Fichtelberg forestry, only the proportion of beech trees at radii of 50 m and 100 m around the tree hollows positively influenced beetle species richness. In the Kelheim forestry, characterized by mixed forest stands, there were no significant interactions between forest structure and species richness of saproxylic beetles. The results show that there are generalizable patterns of local tree hollow characteristics that influence species richness of hollow-dwelling saproxylic beetles across differently structured forest regions, but the importance of these parameters and the influence of forest structure at spatial scales of 50 m - 500 m around the hollows differ strongly, depending on characteristics of the respective forest region.

In the second manuscript I examined the influence of landscape structure at larger spatial scales of 300 m - 5000 m around the focal tree hollows on saproxylic beetle species richness in the hollows in the three study regions Ebrach, Fichtelberg and Kelheim. The study was conducted with the same tree

hollows and with the same saproxylic beetle samples used in the first manuscript. CORINE satellite data were used to relate the proportion of suitable habitat at radii of 300 m - 5000 m around the focal tree hollows to saproxylic beetle species richness in the hollows. Four dispersal-associated functional traits and functional diversity indices of beetles in the hollows were modelled in relation to surrounding landscape structure. The proportion of suitable habitat surrounding the focal tree hollows did not influence total species richness of saproxylic beetles in any of the three study regions but positively affected species richness of threatened species in Ebrach and Fichtelberg across all spatial scales. The analysis of functional diversity indices showed that beetle assemblages in tree hollows shifted toward species with better dispersal abilities when surrounded by a matrix of coniferous forest in the Fichtelberg study region. In contrast, when surrounded by open land in the Kelheim study region, there was no shift toward better dispersal abilities in the hollow-dwelling beetle communities. These results show that threatened saproxylic beetles in tree hollows react more sensitively to surrounding landscape composition than common species and that connectivity of forest patches might greatly support the dispersal of hollow-dwelling saproxylic beetles.

Studies on hollow-dwelling saproxylic insects have mostly focused on beetles. But to gain a holistic understanding of the complex tree hollow habitat and its community composition and diversity it is crucial to also investigate other arthropod taxa and their habitat requirements. Therefore, in the third manuscript, I used DNA metabarcoding to identify all non-beetle saproxylic arthropods emerging from 40 tree hollows in the Ebrach forestry in 2014 and from a subset of 23 tree hollows in 2015. The influence of tree hollow parameters and local forest structure on α- and β-diversity of the most diverse taxa was examined. Parameters influencing α- and β-diversity were different between years and between taxa. The most important parameters were tree hollow volume, entrance area of the hollows and tree circumference. Only β-diversity was also affected by parameters of forest structure, namely amount of dead wood in a 200 m radius (Diptera) and number of tree hollows in a 50 m radius (spiders). We could show the differential habitat requirements of hollow-dwelling saproxylic arthropod taxa and underline the importance of conserving heterogenous tree hollows and related forest structures as habitat for highly diverse saproxylic arthropod communities.

The results of this thesis could fill important knowledge gaps regarding the diversity of saproxylic arthropods in tree hollows and the factors influencing them from small spatial scales to landscape scales and in differently structured forest regions. Using forest inventory data as a new method for the assessment of forest structure and CORINE satellite data for the analysis of large-scale landscape composition proved to be valuable tools. Insights gained from this study should help forest management practitioners, political decision makers and conservationists to make informed decisions on the management of central European forests and the conservation of threatened saproxylic communities in tree hollows.

# Zusammenfassung

Intensive Forstwirtschaft hat in den vergangenen Jahrhunderten zu einem starken Rückgang großer, alter Laubbäume und Totholzstrukturen wie Mulmhöhlen in mitteleuropäischen Wirtschaftswäldern geführt. Folglich sind heute viele Arten saproxyler Arthropoden gefährdet, also Arten, die direkt oder indirekt auf Totholz oder sterbendes Holz oder auf die Anwesenheit anderer Saproxyler angewiesen sind. Mulmhöhlenspezialisten, die auf die Anwesenheit von Mulmhöhlen angewiesen sind, stellen eine besonders bedrohte Gruppe dar; ca. 75% - 86% der auf Mulmhöhlen spezialisierten saproxylen Käferarten in Mitteleuropa sind bedroht. Um die Arthropodengemeinschaften in Mulmhöhlen effektiv schützen zu können, ist es wichtig zu verstehen, welche Eigenschaften von Mulmhöhlen, umgebender Wald- und Landschaftsstruktur die Artenvielfalt höhlenbewohnender saproxyler Arthropoden auf verschiedenen räumlichen Skalen beeinflussen und wie der Einfluss dieser Eigenschaften sich in unterschiedlich strukturierten Waldgebieten und für unterschiedliche höhlenbewohnende Taxa verändert.

Im ersten Manuskript habe ich Eigenschaften von Mulmhöhlen, Höhlenbäumen und umgebender Waldstruktur untersucht, die die Artenvielfalt saproxyler Käfer in Mulmhöhlen in Rotbuchen auf räumlichen Skalen von 50 m - 500 m um die fokalen Mulmhöhlen in den drei Forstbetrieben Ebrach, Fichtelberg und Kelheim beeinflussen. In jedem Waldgebiet wurden 42 - 50 Mulmhöhlen in Rotbuchen mittels Emergenzfallen über die Studiendauer von April bis August 2018 und 2019 untersucht. Als neue Untersuchungsmethode wurden Forstinventurdaten genutzt, die regelmäßig von den Bayerischen Staatsforsten (BaySF) in allen bayerischen Staatswäldern erhoben werden. Insgesamt wurden 283 saproxyle Käferarten (5880 Individuen) gesammelt, von denen 22% bedrohte Arten waren. Die wichtigsten lokalen Parameter, die die Artenvielfalt saproxyler Käfer in allen drei Waldgebieten beeinflussten, waren die Fläche des Höhleneingangs (positiver Einfluss), das Zerfallsstadium des Mulms (negativ) und die Höhe des Höhleneingangs über dem Boden (negativ). Auf Radien von 50 m und 100 m um die Höhlen beeinflusste die Menge an Totholz die Artenvielfalt höhlenbewohnender Käfer im hauptsächlich von Laubwald geprägten Forstbetrieb Ebrach. Im von Nadelwald dominierten Forstbetrieb Fichtelberg zeigte nur der Anteil Buchen auf Radien von 50 m und 100 m um die Mulmhöhlen einen positiven Einfluss auf die Artenvielfalt. Im Forstbetrieb Kelheim, charakterisiert durch gemischte Baumbestände, gab es keine signifikanten Zusammenhänge zwischen Waldstruktur und Artenvielfalt saproxyler Käfer. Die Ergebnisse zeigen, dass es generalisierbare Muster lokaler Mulmhöhleneigenschaften gibt, die die Artenvielfalt saproxyler Käfer in Mulmhöhlen in unterschiedlich strukturierten Waldgebieten beeinflussen, aber die Bedeutung dieser Parameter sowie der Einfluss der Waldstruktur auf räumlichen Skalen von 50 m - 500 m um die Mulmhöhlen unterscheiden sich stark, in Abhängigkeit von den Eigenschaften des jeweiligen Waldgebiets.

Im zweiten Manuskript habe ich den Einfluss der Landschaftsstruktur auf größeren räumlichen Skalen von 300 m - 5000 m um die Mulmhöhlen auf die Artenvielfalt saproxyler Käfer in den Mulmhöhlen in den drei Forstbetrieben Ebrach, Fichtelberg und Kelheim untersucht. Die Studie wurde mit denselben Mulmhöhlen und denselben Käferproben wie die erste Studie durchgeführt. CORINE-Satellitendaten wurden genutzt um den Anteil geeigneten Habitats auf räumlichen Skalen von 300 m - 5000 m um die Mulmhöhlen in Bezug zur Artenvielfalt saproxyler Käfer in den Mulmhöhlen zu setzen. Vier mit Ausbreitungsfähigkeit assoziierte funktionale Merkmale der Käfer in den Mulmhöhlen sowie Indizes der funktionalen Diversität wurden in Abhängigkeit von der umgebenden Landschaftsstruktur modelliert. Der Anteil geeigneten Habitats in der Umgebung der Mulmhöhlen hatte keinen Einfluss auf die Gesamtartenvielfalt der saproxylen Käfer in den untersuchten Waldgebieten, aber beeinflusste die Artenvielfalt bedrohter Arten in Ebrach und Fichtelberg positiv über alle räumlichen Skalen. Die Analyse der funktionalen Diversitätsindizes zeigte, dass sich die Zusammensetzung der Käfergemeinschaften in den Mulmhöhlen, wenn umgeben von einer Matrix aus Nadelwald im Forstbetrieb Fichtelberg, hin zu Arten mit besserer Ausbreitungsfähigkeit veränderte. Im Gegensatz dazu konnte im Forstbetrieb Kelheim, wo Habitatflächen von Offenland umgeben waren, keine erhöhte Ausbreitungsfähigkeit höhlenbewohnender Käfergemeinschaften festgestellt werden. Diese Ergebnisse zeigen zum einen, dass bedrohte saproxyle Käfer in Mulmhöhlen sensibler auf die Zusammensetzung der umgebenden Landschaftsstruktur reagieren und dass Konnektivität von Waldgebieten die Ausbreitung höhlenbewohnender saproxyler Käfer stark unterstützen könnte.

In der Vergangenheit wurden Studien zu höhlenbewohnenden saproxylen Insekten hauptsächlich mit Käfern durchgeführt. Um aber ein ganzheitliches Verständnis des komplexen Habitats Mulmhöhle und der darin lebenden Artengemeinschaften zu erhalten, ist es unerlässlich, auch andere Arthropodentaxa und ihre Habitatansprüche zu untersuchen. Folglich habe ich im dritten Manuskript DNA-Metabarcoding genutzt, um alle saproxylen Nicht-Käfer-Arthropoden zu bestimmen, die im Jahr 2014 aus 40 Mulmhöhlen im Forstbetrieb Ebrach und im Jahr 2015 aus einem Subset aus 23 Mulmhöhlen gesammelt wurden. Der Einfluss von Mulmhöhleneigenschaften und lokaler Waldstruktur auf α- und β-Diversität der artenreichsten Taxa wurde untersucht. Die Parameter, die die α- und β-Diversität beeinflussten, unterschieden sich zwischen den Jahren und zwischen Taxa. Die wichtigsten Parameter waren das Volumen der Mulmhöhlen, die Fläche des Höhleneingangs und der Umfang des Höhlenbaumes. Nur die β-Diversität wurde auch von Parametern der Waldstruktur beeinflusst, nämlich von der Menge an Totholz in einem Radius von 200 m um die Höhlen (Diptera) und von der Anzahl an Mulmhöhlen in einem Radius von 50 m (Spinnen). Wir konnten die unterschiedlichen Habitatansprüche höhlenbewohnender saproxyler Arthropodentaxa aufzeigen und die Wichtigkeit unterstreichen, heterogene Mulmhöhlen und verwandte Waldstrukturen als Habitat vielfältiger saproxyler Arthropodengemeinschaften zu bewahren.

Durch die Ergebnisse dieser Arbeit konnten bedeutende Wissenslücken hinsichtlich der Diversität saproxyler Arthropoden in Mulmhöhlen und deren Einflussfaktoren auf kleinen räumlichen Skalen bis hin zu Landschaftsskalen und in unterschiedlich strukturierten Waldgebieten geschlossen werden. Die Nutzung von Forstinventurdaten als neuer Methode zur Untersuchung der Waldstruktur sowie von CORINE-Satellitendaten zur Analyse der Landschaftszusammensetzung auf großen räumlichen Skalen haben sich als wertvolle Instrumente erwiesen. Erkenntnisse aus dieser Studie sollten eine Hilfe für Forstpraktiker, politische Entscheidungsträger und Umweltschützer darstellen, informierte Entscheidungen bezüglich der Bewirtschaftung mitteleuropäischer Wälder und des Schutzes bedrohter saproxyler Mulmhöhlengemeinschaften treffen zu können.

# Introduction

## History of research on saproxylic insects

The diversity of species associated with dead woody material was noted by many early naturalists (Ulyshen & Ŝobotník 2018). For instance, the Victorian-era naturalist Alfred Russell Wallace collected more than 700 species of beetles at a single location over a two-month period in Singapore which he attributed mostly to the cutting of trees in the area (Wallace 1869). However, it took another 55 years for researchers to describe the succession of insects throughout the wood decomposition process in detail (Blackman & Stage 1924). The 1940s and 50s saw a growing body of literature on insect communities associated with dead wood. However, most of the early research on saproxylic insects focused on the small proportion of species that can pose a threat to forest health, reduce the marketability of timber products, or are pests of wooden structures (Ulyshen & Ŝobotník 2018). In Europe and other temperate zones, wood-boring beetles received the most attention at the time (Hickin 1963). The accumulated knowledge on saproxylic insects let the English ecologist Elton in 1966 conclude that "dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and if (...) removed the whole system is impoverished of perhaps more than a fifth of its fauna" (Ulyshen & Ŝobotník 2018). This important insight has not lost its validity until today as Müller et al. (2008) state that out of all forest species in Germany (excluding plants) approximately 34% are saproxylic, meaning they rely on dead or dying wood, or upon wood-inhabiting fungi, or upon the presence of other saproxylics in at least one stage of their life cycle (Speight 1989). The large body of literature on saproxylic insects can generally be divided into research on social saproxylic insects (mainly termites) and non-social saproxylic insects (Ulyshen & Ŝobotník 2018). In my thesis I focussed on non-social saproxylic insects.

Despite the groundbreaking insights of Elton and fellow researchers the importance of conserving saproxylic assemblages in dead wood has not been recognized by forest practitioners before late in the second half of the 20th century. In the 1970s most forest managers still seemed to be uninformed about the immense value of dead and dying wood for the conservation of forest biodiversity (Stubbs 1972). For many forest managers dead wood resembled the "waste of the woods", lost revenue or the risk of pest outbreaks – concerns still held by many today (Ulyshen & Ŝobotník 2018). Perhaps more than any other work Speight's (1989) report for the Council of Europe brought attention to the challenges saproxylic insects face in European forests after hundreds of years of deforestation, fragmentation, and intensive forest management (Ulyshen & Ŝobotník 2018). The report contained a list of approximately 150 old-growth forests across Europe (mostly in mountainous regions) that were ascribed a high conservation value, meaning they were assumed to be a reservoir for threatened saproxylic insects. According to Speight (1989), these remaining high-value forests, all hundreds or even thousands of years old and isolated from one another, “have effectively become islands within a sea of hostile terrain too vast for saproxylics to successfully traverse” (Ulyshen & Ŝobotník 2018).

Speight’s publication sparked a huge interest in the ecology of dead wood, especially regarding the conservation of saproxylic insects. Hence, the number of publications on the topic grew rapidly in subsequent years and culminated among others in the publication of two excellent books that reviewed the current state of knowledge: Stokland et al. (2012) “Biodiversity in Dead Wood” and Ulyshen (2018) “Saproxylic Insects: Diversity, Ecology and Conservation”. As it became apparent that many species of saproxylic insects were being lost from intensively managed forests, forest managers began focusing more on the conservation of saproxylic species in the last decades (Grove 2002). Today the value of dead wood to biodiversity and nutrient cycling is widely recognized (Ulyshen & Ŝobotník 2018).

## Dead wood - a key resource for forest biodiversity

Dead wood is considered a key resource for biodiversity in forests as it offers habitat and nutritional resources for a great diversity of saproxylic species (Stokland et al. 2012). Saproxylic species are a taxonomically and functionally very diverse group and therefore represent an important component of forest ecosystems (Grove 2002). They include representatives of all major insect orders and can be distinguished into various feeding guilds, i.e., xylophagous, saprophagous, saproxylophagous and xylomycetophagous species, as well as predators and commensals (Quinto et al. 2014). Fungi and beetles are assumed to be the most diverse saproxylic taxa (Siitonen 2012), however, Ulyshen (2018) proposed that dipterans might rival beetles as perhaps the most abundant and diverse order of saproxylic insects. In a study from the northern Rhineland in Germany, 56% of all forest-dwelling beetle species were considered saproxylic (Köhler 2000). Saproxylic beetles represent the most well-studied group of saproxylic insects and have been shown to supply key ecosystem functions in temperate forests, namely representing an important food resource for birds and mammals, directly or indirectly contributing to the decay of dead wood and the cycling of nutrients (Carpaneto et al. 2010; Garcia-Lopez et al. 2016). While fungi and bacteria are the primary decomposers of wood in all ecosystems, some saproxylic roaches and termites are also known to produce the enzymes necessary to break down the three major compounds that comprise the lignocellulose matrix: cellulose, hemicellulose, and lignin (Stokland 2012). However, while the production of enzymes that decompose woody material is widespread among bacteria and fungi, it is very rare among animals (Stokland 2012). Hence, the majority of saproxylic insects that feed on woody material either host protozoan or bacterial symbionts in their digestive tract and exploit their enzymatic activity, or use fungal enzymes obtained from the wood, which stay active in the gut after ingestion (Martin 1991).

### Formation and diversity of dead wood in forest ecosystems

In natural forest ecosystems dead wood is created when trees die or mechanical damage causes injuries to trees (Siitonen 2012). Many natural disturbances can cause injuries to trees including branch and stem breakages by wind, falling trees hitting nearby trees, lightning strikes, wildfires, frost cracks, and snow breakage (Siitonen 2012). Some trees can live out their life spans and then senesce, others die to competition, attack by insects or pathogens, or mechanical damage (Berkov 2018). In extreme cases, entire stands can be transformed into dead wood by large-scale natural disturbances. Wind damage seems to be particularly prevalent, and uprooted trees are especially common at forest edges (D'Angelo et al. 2004). However, in temperate forests, there is seldom a single cause for tree mortality. It is rather a complex and gradual process with multiple contributing factors. Pathogenic fungi and insects often become the final agent that kills the tree when it has already been weakened by other mortality factors, which are often called predisposing factors (Stokland & Siitonen 2012). Even trees that succumb to mechanical damage often appear to have suffered biotic challenges prior to death (Das et al. 2016, Gonzalez-Akre et al. 2016; Berkov 2018).

The way a tree dies has significant influence on the species composition in decaying wood. It makes great difference whether the tree dies suddenly, e.g., because of a storm or wildfire, or whether it dies gradually from drought, competition, or old age (Stokland & Siitonen 2012). Trees that die suddenly have been actively growing until the moment of death, therefore have a rich supply of nutrients in the inner bark which facilitates a diverse subcortical fauna where many saproxylic beetle and dipteran species complete their larval development (Stokland & Siitonen 2012). Such a rapid death of a vital old tree will cause a distinct succession of decay stages of the dead tree over 2-3 decades in the case of beech (Ranius et al. 2009a). On the other hand, trees that are wounded but do not die usually lose some of their bark locally and the trunk is occupied by fungi and saproxylic insects which represents the starting point of tree hollow development (Ranius et al. 2009a; Müller et al. 2014b). Such a slow senescence of a tree over decades will produce an accumulation of different dead wood microhabitats which allows saproxylic species of a variety of niches to co-occur (Stokland & Siitonen 2012; Müller et al. 2014b). Animals that often create such openings in vital trees are woodpeckers (Picidae) (Zahner et al. 2012; Micó 2018) and some beetle species (Buse et al. 2008; Müller et al. 2014b).

The amount and quality of dead wood differ significantly between different forest types. Dead wood amounts are much higher in natural old-growth forests compared to managed forests (Grove 2002). Therefore, the ongoing worldwide conversion of forests from mature to young (<140 years of age) as a result of changes in land use, timber harvesting, insect pests, windthrows and changes in wildfire regimes (McDowell et al. 2020) poses a serious threat to saproxylic species. Many studies have shown a significant positive correlation between dead wood amount and species richness of saproxylic beetles (Grove 2002; Gossner et al. 2013; Floren et al. 2014; Seibold et al. 2017; Haeler et al. 2021). However, total dead wood amount is not a sufficient indicator of saproxylic biodiversity, and additional factors such as type of dead wood (tree species, standing or downed etc.), diameter, sun exposure, degree of decomposition, and distribution of dead wood have all been shown to influence distribution patterns of saproxylic insects (Lassauce et al. 2011; Sverdrup-Thygeson et al. 2014; Müller et al. 2015a, b; Seibold et al. 2016; Vogel et al. 2020). Another important factor influencing the diversity of saproxylic organisms in forests is the range of decomposition stages that occur within dead wood, each providing habitat for different saproxylic assemblages (Grove 2002). As wood decomposes it is colonized by a succession of saproxylic insect species (Blackman & Stage 1924; Kletecka 1996; Hammond et al. 2001; Stokland & Siitonen 2012), as are the fruiting bodies of wood-rotting fungi (Jonsell et al. 1999). Thus, diversity of dead wood, including different types of dead wood and different stages of decomposition, and not just the total amount is important for saproxylic biodiversity as heterogeneity of dead wood habitats in natural forests of ancient times may have led to the vast diversification of saproxylic species (Seibold et al. 2016).

Besides dead wood on the forest floor, there can be a surprising amount of dead wood available high in the air (Berkov 2018). In a study of managed forests in Sweden, the surface area of dead branches attached to living trees was about the same as the surface area of snags, stumps, logs, and branches on the ground (Svensson et al. 2014). In a tropical dry forest in Mexico, more than 70% of the dead woody biomass was standing or attached to living trees (Maass et al. 2002). There are many different dead wood microhabitats within a living, veteran deciduous tree that host different saproxylic species assemblages (Siitonen 2012). Therefore, Speight (1989) coined the term “arboreal megalopolis” as he compared a large-diameter, overmature, veteran deciduous tree containing many different dead wood microhabitats to a city with many distinct neighborhoods. As a deciduous tree ages, parts of it become damaged and die off, therefore providing microhabitats which saproxylic species can colonize, such as dead attached branches, woodpecker holes, various hollows, open wounds surrounded by callus tissue, fruiting bodies of polypore fungi, or dead roots in the soil (Siitonen 2012). Veteran deciduous trees containing such dead wood microhabitats may be commercially overmature but are in the prime of their life with regard to their ecological value (Grove 2002).

## Tree hollows with wood mold - a special type of habitat

Tree hollows represent one of the dead wood microhabitats in living trees and can be located high up in the sunlit tree crown, or on ground-level with connection to the forest floor, or anywhere in between. Kraus et al. (2016) defined five types of tree hollows in temperate European forests: woodpecker holes, insect galleries and bore holes, trunk and mold cavities, branch holes, and dendrotelms (water-filled tree hollows, from the Greek *dendron* = tree, *telm* = pond), each with their own subtypes (Micó 2018).

Ranius et al. (2009a) showed that tree age and diameter were important determinants for the formation of tree hollows as 50% of oak trees (*Quercus robur*) that were 200 - 300 years old in their study in southern Sweden had hollows, while 100% of oak trees over 400 years of age had hollows. Of the oak trees that were less than 100 years old less than 1% had hollows (Ranius et al. 2009a). In fast-growing trees, hollows form at earlier ages than in slow-growing trees, probably due to the fact that hollows are often created when large branches break, and branches are thicker on fast-growing trees in comparison to slow-growing trees of the same age (Ranius et al. 2009a).

Tree hollows in living trees are created when mechanical damage causes injuries of the tree bark and heart-rot fungi access the wood (Siitonen 2012; Micó 2018). Among vertebrates, woodpeckers are the most important ecosystem engineers creating entry holes for bacteria, fungi, and insects (Zahner et al. 2012; Micó 2018). However, the relevance of certain processes for tree hollow development can vary among geographic regions: in Northern America, woodpeckers are very important (Cockle et al. 2011), whereas in Australia the activities of termites and fungi are more important factors for tree hollow formation (Gibbons & Lindenmayer 2002; Ranius et al. 2024). Tree hollows rarely occur in coniferous trees because the strong resin flow of conifers contains phenols and other compounds that are toxic to potential intruders and usually closes injuries of the bark effectively (Siitonen 2012; Milberg et al. 2014). Although fungi are the main decomposers of woody material through enzymatic activity, animals also contribute to the decay process in hollow trees (Gibbons & Lindenmayer 2002). Galleries of wood-boring insects such as beetles and ants facilitate the further spread of wood-decaying fungi and provide access for other species that are unable to excavate their own tunnels (Micó 2018). Saproxylic invertebrates subsequently colonize the heartwood decayed by fungal enzymes, boring into the wood and physically break down the decaying wood, turning the wood into frass (borings and excrements of saproxylic invertebrates) which starts to accumulate at the bottom of the expanding tree hollow (Siitonen 2012). Furthermore, tree hollows with an entrance hole will receive a steady input of organic matter, including dead leaves, twigs and seeds, and vertebrates like birds and mammals can bring in plant and animal debris (Siitonen 2012). The accumulating layer of loose decomposed wood, insect frass and other debris at the bottom of a tree hollow is referred to as wood mold (Ranius & Nilsson 1997; Jönsson et al. 2004).

Tree hollows are characterized by a confined space with unique microclimatic conditions. Similar to cave environments, values of temperature and moisture are generally more constant and stable compared to the surrounding environment (Micó 2018; Schauer et al. 2018b). However, this highly depends on the size of the hollow entrance, depth of the tree hollow, and thickness of the wall of the hollow (Gibbons & Lindenmayer 2002). Tree hollows in large living trees can become an exceptionally long-lasting dead wood microhabitat as they can persist for several hundred years (Siitonen 2012). Mature tree hollows become more structurally complex and should be considered as "multi-habitats" as they offer different resources such as dead wood, saproxylic fungi, sap exudates, and wood mold to the fauna living within (Micó 2018). Nutrient stability is another important feature of tree hollows as bacteria, fungi, and hollow-dwelling animals produce nutrients inside the hollow due to their activity (Jönsson et al. 2004; Micó 2018). Additionally, animal faeces and carcasses can enrich the tree hollows with a considerable nitrogen input (Siitonen 2012). Thus, the nitrogen (N) and phosphorous (P) content of the wood mold at the bottom of the hollow is usually three to six times higher than undecayed wood as a result of the organismal activity (Micó 2018).

### The influence of forest management practices on diversity of hollow-dwelling species

Forest management practices have a high impact on the amount of dead wood and the abundance and diversity of tree microhabitats like tree hollows (Siitonen 2001; Paillet et al. 2010). In past decades intensive forest management has reduced the amount and diversity of dead wood and dead wood-related structures like tree hollows in central European managed forests due to low economical value of veteran deciduous trees (Lindenmayer et al. 2012; Müller et al. 2014b). Moreover, tree hollows mostly occur in deciduous trees that are older than the typical rotation time in wood-production forestry (Ranius et al. 2009a; Ranius et al. 2024). Thus, deciduous trees containing tree hollows have become rare structures in central European managed forests (Lindenmayer et al. 2012; Müller et al. 2014b; Sverdrup-Thygeson et al. 2017). Grove (2002) showed the sensitivity of saproxylic insects to forest management practices, with managed or secondary forests generally supporting fewer individuals, fewer species, and different assemblages compared to old-growth or primary forests. It has been shown that the extinction risk of saproxylic beetles reflects the ecological degradation of forests over the last centuries through forest management (Seibold et al. 2015b). Thus, extinction of saproxylic insect species in central Europe has been mostly driven by intensive forest management (Hanski & Hammond 1995; Siitonen 2001) coupled with the delayed effects of past fragmentation (Grove 2002). Today, efforts are being made in central Europe to protect veteran trees in managed forests, e.g., in non-state forests in Germany through the program of contractual forest conservation (“VNP-Wald”). But veteran deciduous trees containing tree hollows are not only declining in forests. In Europe, Asia and Australia, old deciduous trees persist in traditional agricultural landscapes (Manning et al. 2006; Hartel et al. 2013). Such trees are threatened by abandonment of agricultural land, i.e., changes in land use, as well as intensification of agricultural management which involves clearing of persisting veteran trees (Gibbons et al. 2008; Hartel et al. 2013; Ranius et al. 2024). Hence, saproxylic insects inhabiting tree hollows are one of the most endangered invertebrate groups due to the severe loss of habitat (Seibold et al. 2015b; Lindman et al. 2023). Many populations of invertebrates living in tree hollows are assumed to be declining (Cálix et al. 2018). Highly specialized saproxylic insects are exceptionally threatened, in Germany approximately 75 - 86% of saproxylic beetle species that are dependent on tree hollows are threatened (Floren & Schmidl 2008 [86%]; Schmidl & Büche 2018 [75%]). Since about 10% of all saproxylic beetle species are assumed to be specialized in tree hollows (Ranius et al. 2024), it is evident that hollow trees containing wood mold represent keystone habitats for the conservation of saproxylic species that host many threatened species (Ranius & Jansson 2000; Sirami et al. 2008; Chiari et al. 2012; Gouix et al. 2015; Micó 2018).

### Ecological functions of hollow-dwelling arthropod species

Conservation of saproxylic arthropods in tree hollows can be motivated not only by the value of biodiversity itself, but also because hollow-dwelling saproxylic arthropods fulfill several key ecological functions (Ranius et al. 2024). At least some species act as decomposers, reducing the size of dead wood fragments while increasing N and P concentrations in the hollows (Jönsson et al. 2004; Sánchez et al. 2017; Wetherbee et al. 2022; Ranius et al. 2024). Thereby, these species contribute to the crucial process of element cycling in forests (Grove 2002; Gouix et al. 2015). Moreover, by mechanically degrading dead wood fragments in tree hollows, these species also contribute to the formation and expansion of the hollows (Gibbons & Lindenmayer 2002). Hence, species that act as decomposers in tree hollows can be called ecosystem engineers similar to wood-boring larvae of saproxylic beetles that actively participate in the creation and expansion of the hollows (Buse et al. 2008; Sánchez-Galván et al. 2018; Casula et al. 2021; Fierro et al. 2024). Furthermore, hollow-dwelling arthropods can fulfill ecological functions by influencing nearby ecosystems, e.g., acting as natural enemies in pest control (Wetherbee et al. 2020b; Ranius et al. 2024). Also, saproxylic insects in tree hollows can improve conditions for other hollow-dwelling species. For example, nests of ants in tree hollows can improve thermal conditions for nesting birds (Mitrus et al. 2016; Ranius et al. 2024).

### The influence of characteristics of tree hollows, hollow-bearing trees and local forest structure on diversity of hollow-dwelling species

Among the saproxylic insect species found in tree hollows are facultative species that can also be found in other dead wood structures like tree stumps, logs and snags on the forest floor but also tree hollow specialists that depend on tree hollows (Müller et al. 2014b; Quinto et al. 2014; Taylor & Ranius 2014; Micó 2018; Schauer et al. 2018b). However, not much is known about the specific habitat requirements of most hollow-dwelling saproxylic insects (Ulyshen & Ŝobotník 2018) with the exception of Diptera larvae who dominate assemblages in water-filled tree hollows (dendrotelms) (Srivastava & Lawton 1998; Ulyshen 2018) and a few well-studied saproxylic beetle species that serve as umbrella species for the conservation of tree hollow communities in Europe, like the hermit beetle *Osmoderma eremita* (Jönsson et al. 2004; Ranius et al. 2009b; Chiari et al. 2012; Lindman et al. 2023), or the violet click beetle *Limoniscus violaceus* (Gouix & Brustel 2012; Gouix et al. 2015).

If tree hollows of various sizes and characteristics are available at different strata or heights above the ground, habitat preference of saproxylic insects is likely to be determined by abiotic variables (Berkov 2018) like temperature, pH, humidity, or degree of decomposition of the tree hollow substrate, the wood mold (Micó 2018). Microclimatic conditions within a tree hollow have been shown to be important factors explaining the patterns of saproxylic beetle species' occurrence in tree hollows (Lindman et al. 2023) analogously to the importance of microclimatic conditions for saproxylic beetles in dead wood in general (Müller et al 2014a; Seibold et al. 2016). Tree hollow characteristics that have been shown to influence microclimatic conditions within the hollows include the size of the hollow entrance (Ranius 2002; Quinto et al. 2014; Schauer et al. 2018b; Lindman et al. 2020), the wall thickness of the tree hollow (Gibbons & Lindenmayer 2002), and the amount of wood mold (Ranius et al. 2009b).

To effectively conserve saproxylic communities in tree hollows it is crucial to understand which factors influence the diversity of hollow-dwelling saproxylic arthropods. It has been shown for saproxylic beetles that certain characteristics of tree hollows influence the diversity of beetle assemblages within the hollows (Gouix & Brustel 2012; Quinto et al. 2014; Micó et al. 2015; Schauer et al. 2018b). Among these characteristics are the volume of the tree hollow (positive influence on saproxylic beetle diversity), the size of the hollow entrance (positive influence), the height above ground (negative influence), the temperature inside the hollows (positive influence), and the degree of decomposition of the wood mold inside the hollows (negative or hump-shaped influence) (Ranius 2002; Lindhe et al. 2005; Sverdrup-Thygeson et al. 2010; Widerberg et al. 2012; Müller et al. 2015a; Quinto et al. 2014; Micó et al. 2015; Schauer et al. 2018b). Furthermore, the number of tree hollows in the near surroundings of a focal tree hollow has been shown to positively influence diversity patterns in tree hollows (Ranius & Wilander 2000; Schauer et al. 2018b). However, the direction (positive or negative) in which these factors influence the saproxylic beetle species richness in the hollows is not always unambiguous. For example, threatened saproxylic beetle species in tree hollows have been shown to be associated with warmer temperatures in Scandinavia (Lindhe et al. 2005; Koch Widerberg et al. 2012), but there have also been reports of negative relationships between temperature and occurrence of threatened saproxylic beetles in central and southern Europe (Carpaneto et al. 2010; Schauer et al. 2018b). In southern Europe this finding might be due to the fact that the warmer macro-climate makes hollow-dwelling saproxylic beetles independent of a warm microclimate inside the hollows (Chiari et al. 2012). In central Europe a negative relationship between temperature inside the hollows and diversity of threatened saproxylic beetles in tree hollows may be caused by the strong natural shading of beech trees (Schauer et al. 2018b). These ambiguities illustrate that further research on the factors influencing the composition of saproxylic arthropod assemblages in tree hollows is urgently needed to be able to effectively conserve these threatened communities. Especially in demand are studies that compare the factors that influence the diversity of tree hollow assemblages between different forest regions as it has been shown that differences in forest structure (e.g., tree species composition, amount and distribution of dead wood), land-use history, or climate zone can affect the influence of certain parameters of tree hollows, hollow trees or forest structure on the diversity of saproxylic assemblages in tree hollows (Schauer 2018; Müller et al. 2020). Therefore, I conducted a regional comparison between three forest regions in Bavaria, Germany, regarding the characteristics of tree hollows, hollow trees and local forest structure that influence saproxylic beetle diversity in tree hollows (Henneberg et al. 2021, manuscript 1). As a new method of analysis I used forest inventory data, that is regularly collected by the Bavarian state forest authorities (BaySF), to assess local forest structure in the three study regions Ebrach, Fichtelberg and Kelheim. The three study regions were chosen because they represent different managed forest types in central Europe regarding their forest structure and management regime. Hence, the results are expected to enhance our understanding of how differently structured forest regions vary in the factors that shape saproxylic beetle communities in tree hollows (Henneberg et al. 2021, manuscript 1).

### The influence of large-scale landscape structure on species assemblages in tree hollows

Besides characteristics of tree hollows, hollow trees and forest structure in the direct surroundings of tree hollows, some parameters of large-scale landscape structure have been shown to influence tree hollow assemblages (Micó 2018). Large-scale deforestation and degradation of forests through human land use pose a threat to forest biodiversity in general, but especially affect hollow-dwelling saproxylic species as the number of hollow-bearing veteran trees declines (Bauhus et al. 2009; Lindenmayer et al. 2012), as well as the probability of hollow formation (Remm & Lõhmus 2011). Degradation of forests through human land use has been shown to greatly reduce the amount of dead wood, which in turn significantly alters communities of saproxylic beetles comparable to the loss after natural disturbances (Hammond et al. 2017). Furthermore, fragmentation of forests has been shown to limit movement of tree hollow specialists between remaining forest fragments (Ranius 2002; Khazan et al. 2015; Micó 2018). It has also been shown that some species of hollow-dwelling saproxylic beetles more frequently occur in large forest patches compared to smaller forest fragments, indicating their sensitivity to forest fragmentation (Ranius 2002). However, some species of threatened saproxylic beetles have been shown to not rely on large old-growth forest regions, but rather on habitat continuity in the form of single old veteran trees containing hollows in rural avenues, urban parks, or agricultural landscapes (Oleksa & Gawroński 2006; Oleksa et al. 2015; Micó 2018). This indicates that different organisms have widely different abilities to survive in a specific landscape over a given period of time, depending on their habitat demands, reproductive modes and dispersal abilities (Sverdrup-Thygeson et al. 2014). The sensitivity of species to changes in landscape composition, such as a reduction in habitat amount below a critical threshold of remaining habitat, is closely related to species' traits (e.g., dispersal ability, reproduction, edge sensitivity) and landscape characteristics (e.g., degradation, fragmentation, rate of changes in land use) (Swift & Hannon 2010; Sverdrup-Thygeson et al. 2014). But except for a few well-studied "umbrella species" (e.g., *Osmoderma eremita, Limoniscus violaceus*), a knowledge gap exists regarding the sensitivity of hollow-dwelling saproxylic species towards the surrounding landscape structure (Eckelt et al. 2018). Studies are lacking that compare the effects of landscape structure at large scales of several kilometers around the focal tree hollows on tree hollow communities in differently structured forest regions. Therefore, we used satellite imagery of the European Environment Agency (Copernicus Programme) to compare the influence of the surrounding landscape composition at spatial scales of 300 m - 5000 m around the focal tree hollows in the three study regions Ebrach, Fichtelberg and Kelheim on saproxylic beetle species richness within the hollows (Henneberg et al. 2025; manuscript 2).

## Dispersal ability of saproxylic beetles and how it affects saproxylic communities in tree hollows

Habitat loss and habitat fragmentation pose a huge threat for saproxylic insects that are dependent on tree hollows as species specialized in stable and long-lasting habitats are assumed to have rather low dispersal abilities (Nilsson & Baranowski 1997; Travis & Dytham 1999; Hedin et al. 2008; Oleksa et al. 2013; Percel et al. 2019). Accordingly, many saproxylic beetle species specialized in tree hollows seem not to be able to overcome the distances between unconnected forest regions by dispersal (Ranius & Hedin 2001; Hedin et al. 2008; Jonsson 2012; Oleksa et al. 2015). Dispersal ability is a very important trait of species facing the threat of habitat loss or habitat fragmentation (Thomas 2000). Dispersal is crucial to ensure gene flow between patchy habitats like tree hollows, allows the colonization of new habitats, and therefore affects species' distribution patterns, metapopulation structure, and the extinction risk of populations (Hanski et al 1994; Bowler & Benton 2005; Feldhaar & Schauer 2018). Recent studies on genetic population structure of saproxylic insects imply that many species might not be as dispersal-limited as it has been assumed in the past (Schauer et al. 2018a; Feldhaar & Schauer 2018). For example, it has been shown that *Rosalia alpina* (Coleoptera: Cerambycidae), a threatened large-bodied saproxylic beetle in Europe, can cover large distances of at least 1.6 km by flight (Drag et al. 2011). Even larger dispersal distances of up to 170 km that have been shown for some species of saproxylic beetles (Nilssen 1984) are to a large part the result of small-bodied species' passive dispersal by wind (Jonsson 2003). Such passive dispersal is unlikely in large species like *Rosalia alpina*, and their mobility presumably is much lower (Drag et al. 2011; Feldhaar & Schauer 2018). Moreover, dispersal distances that have been proposed for saproxylic beetles in various studies depend a lot on the underlying sampling methods and can easily be under- or overestimated. For example, studies conducted on the dispersal ability of the saproxylic beetle *Bolitophagus reticulatus* using the mark-recapture method have resulted in very limited dispersal distances of a few meters (Nilsson 1997), while flight-mill experiments with the same species have resulted in median dispersal distances of 7 km (Jonsson 2003), and genetic studies implied dispersal distances of tens of kilometers (Jonsson et al. 2003).

Many threatened saproxylic beetle species seem to show life-history traits that make these species less adapted to effectively disperse and colonize patchy habitats like fruiting bodies of saproxylic fungi or tree hollows compared to closely related common species (Jonsson 2003; Feldhaar & Schauer 2018). However, not much is known about dispersal abilities of hollow-dwelling saproxylic species except for a few well-studied beetle species (Feldhaar & Schauer 2018). I addressed this knowledge gap by assessing functional diversity indices of morphological traits that are associated with dispersal ability in a landscape-scale study on hollow-dwelling saproxylic beetles in the three forest regions Ebrach, Fichtelberg and Kelheim (Henneberg et al. 2025; manuscript 2). With this study I set out to answer the questions if threatened, and presumably more dispersal-limited saproxylic beetle species in tree hollows react more sensitively to the proportion of habitat available in the surrounding landscape, and if tree hollow communities in more isolated forest patches shift in their species composition towards species with better dispersal abilities (Henneberg et al. 2025; manuscript 2).

## Diversity of non-beetle saproxylic arthropods in tree hollows

Tree hollows are more diverse functionally and taxonomically than any other dead wood habitat (Müller et al. 2014b; Micó 2018). But knowledge on the composition of insect assemblages in tree hollows varies greatly among taxa and regions (Micó 2018). Although density of tree hollows increases from the poles to the equator (Boyle et al. 2008; Vázquez & Renton 2015), insect assemblages in tree hollows have been poorly studied in tropical regions, with the exception of water-filled tree hollows (dendrotelms) (Fincke 1999; Grove & Stork 1999; Seibold et al. 2015a; Micó 2018). Most studies on insect assemblages in tree hollows have been conducted in Europe, in both temperate and Mediterranean forests (Ranius & Jansson 2000; Quinto et al. 2014; Micó et al. 2015; Sverdrup-Thygeson et al. 2017; Sánchez-Galván et al. 2018; Schauer et al. 2018b).

An important knowledge gap in the study of insect diversity in tree hollows occurs at a taxonomical level. At least 14 orders of insects have been reported from tree hollows (Micó 2018). Among them, saproxylic beetles represent by far the best-studied order with more than 64 families and over 700 species reported from tree hollows, most of them associated with different types of tree hollows (Micó 2018). The most diverse beetle families in tree hollows are Tenebrionidae, Staphylinidae, Elateridae, Scarabaeidae, Histeridae, Ptiliidae, Ciidae and Curculionidae (Park & Auerbach 1954; Gimmel & Ferro 2018). Besides beetles the most diverse order of insects in tree hollows are Diptera. While saproxylic Diptera are poorly known compared to saproxylic beetles and often underestimated in dead wood (Rotheray et al. 2001), at least 12 families and more than 48 species have been reported from tree hollows (Micó 2018). Among them, hover flies (Syrphidae) are the most diverse family, but species often found in or specialized in tree hollows also include some crane flies (Tipulidae), wood soldier flies (Xylomyidae), long-legged flies (Dolichopodidae) and stiletto flies (Therevidae) (Andersson 1999; Alexander 2002; Siitonen 2012). Reports from other insect orders in tree hollows are still scarce except for ants (Hymenoptera) and termites (Blattodea) in certain latitudes and dragonfly (Odonata) larvae in water-filled tree hollows in the tropics where they predate mosquito larvae (Fincke 1999; Gibbons & Lindenmayer 2002; Micó 2018). It has been reported that the most abundant taxa in the wood mold at the bottom of tree hollows are springtails (Collembola) and mites (Arachnida: Acari) (Micó 2018). Furthermore, it has been shown that there is a specialized oribatid mite (Acari: Oribatida) fauna living in tree hollows that differs from mite communities in the soil (Behan-Pelletier & Walter 2000; Taylor & Ranius 2014). This finding exemplifies the high conservational value of tree hollows for a great diversity of taxa. Furthermore, there can be considerable turnover in the species composition emerging from a single tree hollow between years (Schauer et al. 2018b), making it even harder to comprehensively study insect assemblages in tree hollows. Predatory behavior seems to be very noteworthy within tree hollows as more than 30% of the identified species in a study from Spain were predators (Quinto et al. 2014).

Hollow-dwelling Staphylinidae beetles of the subfamily Pselaphinae have been described as tree hollow specialists predating mites and collembolans (Park & Auerbach 1954). Other predatory arthropods such as spiders (Araneae) and pseudoscorpions (Pseudoscorpionida) are also important members of invertebrate assemblages in tree hollows (Ranius & Wilander 2000; Martínez-Devesa et al. 2024).

I want to contribute to closing the taxonomical knowledge gap with the third manuscript of this thesis where I used high-throughput DNA metabarcoding to determine all non-beetle saproxylic arthropods that emerged from the examined tree hollows (Schauer, Henneberg et al. 2025; manuscript 3). To my knowledge, this is the first time that DNA metabarcoding has been used to study non-beetle saproxylic arthropods emerging from tree hollows in central European forests.

# Objectives

1. In the first manuscript I examined the influence of local characteristics of tree hollows, hollow-bearing trees and parameters of the surrounding forest structure at small spatial scales on species richness of hollow-dwelling saproxylic beetles in the three forest regions Ebrach, Fichtelberg and Kelheim. Forest structure was investigated at spatial scales of 50 m - 500 m around the focal tree hollows by using forest inventory data collected by the Bavarian state forest authorities (BaySF) as a new method of analysis. I conducted a regional comparison and validation of the results that Schauer et al. (2018) obtained in the Ebrach forestry (Steigerwald, Germany) in the three forest regions Ebrach, Fichtelberg and Kelheim that are characterized by different forest structure, tree-species composition and management regime (manuscript 1).
2. In the second manuscript I widened the spatial scale of the study to a landscape perspective by utilizing CORINE satellite imagery to assess the influence of the surrounding landscape composition at larger spatial scales of 300 m - 5000 m around the focal tree hollows on patterns of saproxylic beetle species richness and dispersal-associated functional traits within the hollows (manuscript 2).
3. In the third manuscript I used high-throughput DNA metabarcoding to study α- and β-diversity of saproxylic taxa in tree hollows that are less well-known compared to saproxylic beetles. I compared the findings regarding the most diverse taxa to the literature on saproxylic and hollow-dwelling taxa and discussed whether the same factors that influence α- and β-diversity of saproxylic beetles in tree hollows also influenced the diversity of the lesser-known hollow-dwelling taxa in the study (manuscript 3).
4. I make recommendations on forest management based on the results of the manuscripts, with the aim to conserve the highly threatened tree hollow communities.

# Manuscripts and declaration of own contribution

**Manuscript 1:**

Title: **Influence of tree hollow characteristics and forest structure on saproxylic beetle diversity in tree hollows in managed forests in a regional comparison.**

Authors: Benjamin Henneberg, Simon Bauer, Markus Birkenbach, Vanilla Mertl, Manuel J. Steinbauer, Heike Feldhaar, Elisabeth Obermaier.

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Own contribution: data acquisition: 75%, data analysis and figures: 60%, writing: 85%, concept and discussion: 50%; corresponding author.

BH, EO and HF conceived the ideas and designed the methodology. BH, SB, MB and VM collected the data. BH, SB, MB, VM and MJS analyzed the data. BH, SB, MB, VM, HF and EO interpreted and discussed results. Figures and tables were created by BH, SB, MB, VM and MJS. BH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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RESEARCH ARTICLE

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# Influence of tree hollow characteristics and forest structure on saproxylic beetle diversity in tree hollows in managed forests in a regional comparison

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## Abstract

Tree hollows are among the rarest habitats in today's Central European managed forests but are considered key structures for high biodiversity in forests. To analyze and compare the effects of tree hollow characteristics and forest structure on diversity of saproxylic beetles in tree hollows in differently structured managed forests, we examined between 41 and 50 tree hollows in beech trees in each of three state forest management districts in Germany. During the two-year study, we collected 283 saproxylic beetle species (5880 individuals; 22% threatened species), using emergence traps. At small spatial scales, the size of hollow entrance and the number of surrounding microhabitat structures positively influenced beetle diversity, while the stage of wood mould decomposition had a negative influence, across all three forest districts. We utilized forest inventory data to analyze the effects of forest structure in radii of 50–500 m around tree hollows on saproxylic beetle diversity in the hollows. At these larger spatial scales, the three forest management districts differed remarkably regarding the parameters that influenced saproxylic beetle diversity in tree hollows. In Ebrach, characterized by mostly deciduous trees, the amount of dead wood positively influenced beetle diversity. In the mostly coniferous Fichtelberg forest district, with highly isolated tree hollows, in contrast, only the proportion of beech trees around the focal tree hollows showed a positive influence on beetle diversity. In Kelheim, characterized by mixed forest stands, there were no significant relationships between forest structure and beetle diversity in tree hollows. In this study, the same local tree hollow parameters influenced saproxylic beetle diversity in all three study regions, while parameters of forest structure at larger spatial scales differed in their importance, depending on tree-species composition.

KEYWORDS

Coleoptera, conservation, dead wood, threatened species, tree hollows, wood mould

## 1 | INTRODUCTION

Recent studies have shown that the abundance and species richness of insects have declined strongly over past decades (Wagner, 2020). This is reported for agricultural landscapes (Wagner, 2020) as well as managed forest ecosystems (Seibold et al., 2019). Intensive forest management has resulted in a massive decline of key elements important for forest biodiversity, such as dead or moribund trees (Vogel et al., 2020). Dead wood is a characteristic and abundant resource in natural forest ecosystems (Seibold & Thorn, 2018) but is often removed in European managed forests (Thorn et al., 2020), resulting in low amounts of dead wood (Gossner, Lachat, et al., 2013; Thorn et al., 2020). Reducing the amount of dead wood in managed forests can help lowering the risk of natural disturbances like wildfires through fuel reduction or pest insect outbreaks (Leverkus et al., 2020). However, this practice also eliminates important habitat features for saproxylic taxa (Thorn et al., 2016). Consequently, many species of saproxylic insects, which directly or indirectly depend on dead wood in at least one stage of their life cycle (Speight, 1989), have become endangered or extinct (Seibold et al., 2015; Thorn et al., 2020). Since approximately 34% of forest-dwelling species in Europe are regarded as saproxylic (Müller et al., 2008), this also contributes to the decline of forest biodiversity in general. Beetles are especially threatened as >50% of all forest-dwelling beetle species in Germany are regarded as saproxylic (Köhler, 2000).

Large old trees containing tree hollows are among the rarest structures in European managed forests (Lindenmayer et al., 2012). Tree age and diameter are important factors that facilitate the development of tree hollows (Ranius et al., 2009). In contrast to other dead wood structures like logs, tree hollows provide long-lasting microhabitats that offer nutritional resources for many species of saproxylic organisms (Siitonen, 2012), and a specific abiotic environment characterized by stable temperature and moisture conditions and increased pH values (Müller et al., 2014). Each tree hollow is unique with regard to the combination of microenvironmental characteristics and the range of microhabitats within (Quinto et al., 2014; Siitonen, 2012). Besides dead wood generalists, tree hollows also provide habitat for many highly specialized saproxylic beetle species (Speight, 1989). These cavity-dependent tree hollow specialist species complete most of their life cycle in tree hollows and represent an exceptionally threatened group with approximately 75% of them being considered to be threatened or endangered (Schmidl & Büche, 2018).

In past decades European forests were mainly managed for timber production. Since the late 1990s, biodiversity conservation programs with a special focus on dead wood structures have been implemented in an increasing number of European countries, including Finland, Sweden, and Germany (Thorn et al., 2020; Vítková et al., 2018). However, to implement effective conservation measures it is crucial to better understand which forest parameters are the most important to enhance saproxylic beetle diversity. While several studies have analyzed the habitat requirements of saproxylic beetles in general (Müller et al., 2015; Ranius et al., 2015; Seibold et al., 2016), less is known about beetle communities in tree hollows (Micó, 2018; Micó et al., 2015; Quinto et al., 2014; Schauer et al., 2018). Besides limited habitat availability, many saproxylic beetles are assumed to have limited dispersal abilities (Feldhaar & Schauer, 2018). Therefore, it is important to analyze the influence of forest parameters on saproxylic beetle diversity in tree hollows at different spatial scales (Ranius et al., 2015), from characteristics of the tree hollows themselves (Quinto et al., 2014; Schauer et al., 2018), to parameters of forest structure such as distribution of dead wood, age structure, and tree-species composition (Floren et al., 2014; Gossner et al., 2013; Micó et al., 2013).

The aim of this study was to assess the influence of parameters of tree hollows and the surrounding forest structure on the diversity of saproxylic beetles in tree hollows at different spatial scales. We conducted our study in a regional comparison to achieve generalizable results and to investigate possible regional differences. We selected three state forest regions in Bavaria, Germany, that differed in tree-species composition but were all representative for Central European managed forests. In addition to local parameters of tree hollows and surrounding forest structure we recorded in the field, we used forest inventory data that are collected systematically for all state forest regions by the Bavarian state forest authority (BaySF) and other German state forest authorities. The use of forest inventory data allowed us to statistically analyze parameters of forest structure at larger spatial scales around the focal tree hollows.

Here we address the following questions: (I) Which parameters of tree hollows and forest structure of managed forests are related to species richness of saproxylic beetles in tree hollows of beech trees at different spatial scales? Based on existing studies we hypothesize that local tree hollow parameters like area of hollow entrance (Quinto et al., 2014) or temperature inside the hollows (Müller et al., 2015; Schauer et al., 2018) as well as early to intermediate stages of wood mould decomposition (Schauer et al., 2018) will positively influence saproxylic beetle species richness, while the amount of dead wood might positively influence beetle species richness at larger spatial scales (Müller et al., 2015). (II) Are there common parameters explaining species richness of hollow-using beetles across all three forest regions? We hypothesize that local tree hollow parameters might be more influential to saproxylic beetle species richness than parameters of forest structure at larger spatial scales as the quality of tree hollows is crucial for the development of beetle individuals. Tree hollows provide nutritional resources as well as a diversity of microhabitats suitable for the development of saproxylic beetles while parameters of forest structure at larger spatial scales might be more important for accessibility of tree hollows and population sizes of saproxylic beetles.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

The study was conducted in 2018 and 2019 in three Bavarian state forest management districts (Bayerische Staatsforsten, BaySF):

Ebrach (N 49°50′, E 10°29′), Fichtelberg (N 49°59′, E 11°50′), and Kelheim (N 48°55′, E 11°52′). These forest management districts were chosen because they represent typical managed forest types in Central Europe as they display the full range of management intensity from strict forest reserves to intensively managed forests (Gossner, Lachat, et al., 2013). The study regions also represent a gradient in tree-species composition from semi-natural beech forests (Ebrach) to mixed forests (Kelheim) and forests with a high proportion of planted *Picea abies* trees (Fichtelberg) that is typical for Central European managed forests (Müller et al., 2008).

The forest management district Ebrach in northern Bavaria consists of temperate deciduous forest stands (app. 1000 $km^2$, low mountain range, mean annual temperature: 7–8°C, mean annual precipitation: 850 mm [Bässler et al., 2014]). The dominant tree species is beech *Fagus sylvatica* (43% cover), followed by oak (*Quercus robur* and *Quercus petraea*, 20%). Deciduous trees cover more than 70% of the forest area (Müller et al., 2008). The altitude of sample trees ranged from 324 to 482 m a.s.l.

The forest management district Fichtelberg, located in the low mountain range Fichtelgebirge, consists of mainly coniferous forest stands (app. 157 $km^2$, mean annual temperature: 5–6°C, mean annual precipitation: 1000–1500 mm [BaySF, 2017]), and is characterized by humid, sub-alpine climate. The dominant tree species is spruce *P. abies* (80% cover), followed by beech (7%) (BaySF, 2017). The altitude of sample trees ranged from 525 to 873 m a.s.l.

The forest management district Kelheim consists of mixed forest stands (app. 179 $km^2$, mean annual temperature: 7–8°C, mean annual precipitation: 650–850 mm [BaySF, 2015]), and is characterized by sub-oceanic climate. Its forest stands are mixed in tree-species composition with 56% coniferous and 44% deciduous trees. The dominant tree species is spruce (44% cover), followed by beech (29%) (BaySF, 2015). The altitude of sample trees ranged from 396 to 566 m a.s.l.

We selected between 41 and 50 beech trees with tree hollows in each forest management district (Ebrach: 50, Fichtelberg: 43, Kelheim: 41) that were distributed over the whole area of each management district (Figures A1–A3). Tree hollows were selected if they contained at least 2 cm of wood mould at the bottom of the hollow, and the diameter at breast height (DBH) of the host tree was at least 20 cm. Only tree hollows with a maximum height above ground of the lowest point of the hollow entrance of 350 cm were sampled. The minimum distance between two sample trees was 200 m, and the minimum distance to the forest edge was 100 m. We randomly selected tree hollows matching the criteria in each forest stand by assigning each tree hollow in a given stand a number and rolling a dice.

## 2.2 | Sampling method and identification of saproxylic beetles

After selection in February and March (Ebrach/Fichtelberg: 2018, Kelheim: 2019), all tree hollows were closed with black acrylic mesh to prevent vertebrates like birds from using them as nesting place. The black acrylic mesh also did not allow insects to pass. During the sampling period from April to September (18 weeks), all tree hollows were closed with black fabric and emergence traps (modified from Gouix & Brustel, 2012) (Figure A4) that allow efficient sampling of tree hollow arthropod communities as only individuals emerging from the tree hollows will be trapped (Schauer et al., 2018). The collecting bottles contained 99.8% ethanol and were emptied biweekly. A beetle taxonomist (Boris Büche) identified all beetles to species-level.

## 2.3 | Parameters of tree hollows/hollow-bearing trees recorded in the field

The following parameters of each tree hollow/hollow-bearing tree were recorded:

- *Area of hollow entrance* calculated as the area of an ellipse with $A = \pi * a * b$, where $a$ is half the height and $b$ half the width of the hollow entrance.
- *Hollow volume* calculated as the volume of a cylinder with $V = \pi * r^2 * h$, where $r$ is the internal radius of the hollow measured at the entrance and $h$ the internal height of the hollow measured with a telescopic measuring stick.
- *Height above ground* measured as distance of the lowest point of the hollow entrance to the ground.
- *Diameter at breast height (DBH)* of the hollow tree measured at 130 cm above ground.
- *Height above sea level*: altitude of each tree hollow in m a.s.l.
- *Stage of decomposition*: the stage of decomposition of wood mould sampled from the base of each tree hollow at a depth of 2–5 cm, using a spoon that was attached to a stick, was determined using three parameters, color, texture, and visible woody parts, and was classified in four ascending categories according to Jarzabek (2005):
  *Stage 1/low decay:* yellow to light brown in color, visible woody parts of bigger size.
  *Stage 2/medium decay:* light brown to brown in color, visible woody parts of smaller size.
  *Stage 3/medium to high decay:* brown to dark brown in color, almost no visible woody parts.
  *Stage 4/high decay:* dark brown to black in color, no visible woody parts.
- *Temperature inside the hollow* measured with temperature loggers inside each tree hollow every 60 min over the whole sampling period.

## 2.4 | Parameters of forest structure recorded in the field

Two parameters of forest structure were recorded around each tree hollow:

- *Surrounding microhabitat structures*: the number of microhabitat structures in trees according to Kraus et al. (2016) in a 30 m radius around each tree hollow: woodpecker holes, visible tree fungi, broken branches with a minimum diameter of 12 cm, and injuries to the bark with a minimum area of 250 $cm^2$. These tree-related microhabitat structures have been widely recognized as important substrates and structures for saproxylic biodiversity in forests and are receiving increasing attention in management, conservation and research (Larrieu et al., 2018).
- *Surrounding tree hollows*: the number of visible tree hollows in a 30 m radius around each tree hollow.

## 2.5 | Parameters of forest structure assessed via forest inventory data

We used forest inventory data collected by the Bavarian state forest authorities (BaySF) in 2010–2012. Sampling of forest inventory data is conducted every 10 years by the BaySF on a 200 × 200 m grid over the whole area of the forest management district, with a sampling point at each nodal point. More than 100 parameters are recorded within a parameter-dependent radius around each sampling point, out of which we chose those that we expected to influence saproxylic beetle diversity: *amount of dead wood* (volume of all dead woody parts, standing or downed, with a minimum diameter of 20 cm), sampled within a radius of 12.62 m (500 $m^2$) around each sampling point, and *DBH of deciduous trees* (the mean diameter at breast height in cm) as a proxy for age structure of deciduous trees, also sampled within a radius of 12.62 m (500 $m^2$) around each sampling point. Additionally, in the forest management district Fichtelberg that consisted mainly of coniferous trees, we examined the *proportion of beech trees*. For parameters *DBH of deciduous trees* and *proportion of beech trees*, only trees assigned to the upper forest layer were included in the analysis to avoid overrepresentation of young trees that lack suitable microhabitats for saproxylic beetles.

## 2.6 | Interpolation of forest inventory data

Because forest inventory data is recorded as point data, it must be interpolated to maps with a continuous spatial distribution prior to regression analysis with species richness of saproxylic beetles. We tested the forest inventory parameters for spatial autocorrelation by visually inspecting semivariograms in the software ArcGIS (ESRI, 2018). The only parameter of forest inventory data where we detected spatial autocorrelation and that also had a normal distribution, and we therefore were able to apply the geostatistical Kriging approach was *DBH of deciduous trees* in the forest management district Ebrach. For all other forest inventory parameters and forest management districts we applied the deterministic inverse distance weighting (IDW) method to spatially interpolate forest inventory data and create interpolation maps (Figures A5–A6).

## 2.7 | Statistical analysis of forest inventory data

Interpolation maps displaying forest inventory parameters cannot be directly used for statistical analysis as they display a spatially continuous data distribution. To obtain values for each sampled tree hollow we used the software ArcGIS (ESRI, 2018) to transform the interpolated data to a point grid of 10 × 10 m. We drew circular buffers around each tree hollow with radii ranging from 50 to 500 m and calculated the average value for each forest inventory parameter within each buffer. We used these values for the statistical analysis to examine the forest inventory parameters at different spatial scales around each tree hollow. We randomly excluded buffer sizes or single tree hollows from the analysis when there was more than 10% overlap of the buffer areas of neighboring tree hollows or with the border of the forest management district.

## 2.8 | Statistical analysis

To visualize similarities in species composition between the three study sites, detrended correspondence analysis (DCA) was performed using the R function *decorana* in the *vegan* package (Oksanen et al., 2013). To analyze the influence of tree hollow parameters and parameters of forest structure on species richness of hollow-using beetles, generalized linear models (GLMs) with Poisson error distribution were implemented. Collinearity among explanatory variables was tested using Pearson's linear correlation (exclusion criterion for two variables in the same model $|r| > .7$). Univariate GLMs were used for preselection of explanatory variables for multivariate GLMs. All explanatory variables with significant influence on species richness in univariate GLMs were used in combination with forest inventory data in multivariate GLMs. If two variables showed collinearity they were used in separate models. If there were no local tree hollow parameters with significant influence on species richness in univariate GLMs, the four parameters with the lowest *p*-values were selected for multivariate GLMs. To improve model fitting and the distribution of residuals all explanatory variables were transformed. Depending on the data distribution, either a log- or sqrt-transformation was chosen. By visually inspecting the distribution of residuals in univariate GLMs the model fit of transformed variables was compared to the untransformed variables, and the version that provided the best distribution of residuals was selected for multivariate GLMs. Stepwise model selection based on AIC was used to remove non-relevant variables from the models (R function *step* in the *stats* package). All multivariate models were tested for overdispersion using the R function *dispersion.test* in the *AER* package (Kleiber & Zeileis, 2008). Each explanatory variable that showed significant influence on species richness in multivariate GLMs was visualized using the R package *visreg* (Breheny & Burchett, 2017). Analyses were performed for total species richness of saproxylic beetles as well as for the subset of threatened species (i.e. species listed with a status of 0–3 on the Red List of Germany (Schmidl & Büche, 2018)).

To combine all three forest management districts in a single model we created generalized linear mixed-effects models (GLME) using the R function *glmer* in the *lme4* package (Bates et al., 2015), with parameters of tree hollows and forest structure as fixed factors and forest management district as the random factor. Residuals of random factors were examined visually by inspecting the fitted vs. residuals plot (R function *plot* in the *lme4* package [Bates et al., 2015]) and the residuals vs. predicted plot (R function *simulateResiduals* in the *DHARMa* package [Hartig, 2020]). All analyses were performed with the software R, version 3.6.3 (R Core Team, 2020).

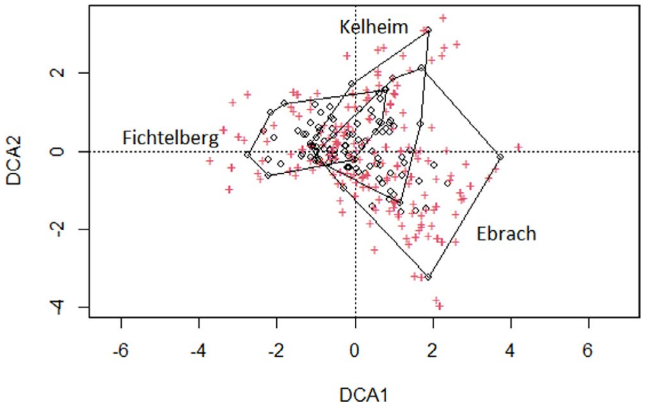

**FIGURE 1** Detrended correspondence analysis (DCA) that visualizes similarities in species composition between the three study sites; circles = tree hollows, crosses = saproxylic beetle species

## 3 | RESULTS

### 3.1 | Saproxylic beetles

In the three forest management districts (134 tree hollows), we collected a total of 5880 saproxylic beetle individuals, belonging to 283 species and 48 families. Sixty-two species (21.9%) are regarded as threatened (Schmidl & Büche, 2018). Four species of the collected beetle species are critically endangered (Red List of Germany status 1 [Schmidl & Büche, 2018]): *Ampedus brunnicornis*, *Crepidophorus mutilatus*, *Cryptophagus deubeli*, *Prionychus melanarius*. The sampled species are very diverse regarding body size (ranging from 1–2 mm to approximately 5 cm) and ecological guild (Schmidl & Bußler, 2004). Only few species are flightless; the majority is mobile. However, for most species it is not known if they are highly mobile or more or less sessile, and how far they disperse within a forest or even between forest regions (Feldhaar & Schauer, 2018).

In 2018 we collected 4151 individuals in Ebrach (50 tree hollows), belonging to 196 species from 43 families with 41 species (20.9%) being regarded as threatened. The same year we collected 441 individuals in Fichtelberg (43 tree hollows), belonging to 74 species from 24 families with nine species (12.2%) being regarded as threatened. In 2019 we collected 1288 individuals in Kelheim (41 tree hollows), belonging to 107 species from 32 families with 28 species (26.2%) being regarded as threatened. The average species richness of saproxylic beetle species per tree hollow was 13.2 ± 6.0 (mean ± SD) in Ebrach, 4.6 ± 2.7 in Fichtelberg, and 7.9 ± 3.7 in Kelheim. Similarities in species composition between the three study sites were visualized using detrended correspondence analysis (DCA) (Figure 1).

### 3.2 | Effects of tree hollow characteristics and forest structure on saproxylic beetle diversity

### 3.2.1 | Forest management district Ebrach

In Ebrach species richness of saproxylic beetles was negatively related to the height of the tree hollows above ground ($z = -2.31$, $p < .05$), and to the *stage of decomposition* of the wood mould inside the hollows ($z = -2.82$, $p < .001$). There was a hump-shaped relationship to *temperature* inside the hollows ($z = 3.82$, $p < .001$). This relationship turned positive in the $r = 500$ m model. Furthermore, representing forest structure at larger spatial scales, the number of microhabitat structures in a 30 m radius around the tree hollows (*surrounding microhabitat structures*, $z = 2.32$, $p < .05$), and the amounts of dead wood up to a radius of 100 m around the tree hollows (*dead wood volume*, $r = 50$ m, $z = 3.24$, $p < .01$; $r = 100$ m, $z = 2.72$, $p < .01$) were positively correlated with the total number of saproxylic beetle species in the tree hollows (Figure 2, Table A1). Pseudo-$r^2$ values that show the explanatory power of the models range from 0.378 to 0.740 depending on radius (Table A1).

When only the 41 threatened saproxylic beetle species were included in the analysis, the volume of the tree hollows ($z = 3.21$, $p < .01$) was the only local tree hollow parameter that was positively correlated with the number of beetle species. The height of the hollow entrance above ground ($z = -2.60$, $p < .01$) and the *stage of decomposition* of the wood mould ($z = -2.70$, $p < .01$) were negatively correlated with the number of species. The number of microhabitat structures in a 30 m radius around the tree hollows (*surrounding microhabitat structures*, $r = 30$ m, $z = 3.24$, $p < .01$) was the only parameter of forest structure that was positively correlated with the number of threatened saproxylic beetle species (Figure A7, Table A2). Pseudo-$r^2$ values that show the explanatory power of the models range from 0.288 to 0.691 depending on the radius (Table A2).

### 3.2.2 | Forest management district Fichtelberg

In Fichtelberg species richness of saproxylic beetles was positively related only to the proportion of beech trees in the tree-species composition at different spatial scales around the tree hollows (*proportion of beech trees*, $r = 50$ m, $z = 2.27$, $p < .05$; $r = 100$ m, $z = 2.28$, $p < .05$)

(Figure 3, Table A3). Thus, with increasing proportion of beech trees in the surrounding of tree hollows, the total number of hollow-using beetle species increased in this conifer dominated forest area. Pseudo-$r^2$ values that show the explanatory power of the models are 0.113 ($r = 50$ m) and 0.116 ($r = 100$ m) (Table A3).

When only the nine threatened saproxylic beetle species were included in the analysis, species richness was positively related to the number of microhabitat structures in a 30 m radius around the tree hollows (*surrounding microhabitat structures*, $r = 30$ m, $z = 2.19$, $p < .05$) and again the *proportion of beech trees* up to a radius of 100 m around the focal tree hollows ($r = 50$ m, $z = 2.54$, $p < .05$; $r = 100$ m, $z = 2.50$, $p < .05$) (Figure A8, Table A4). Pseudo-$r^2$ values that show the explanatory power of the models range from 0.203 to 0.487 depending on radius (Table A4).

### 3.2.3 | Forest management district Kelheim

In Kelheim species richness of saproxylic beetles showed a U-shaped relationship to the size of the *area of hollow entrance*

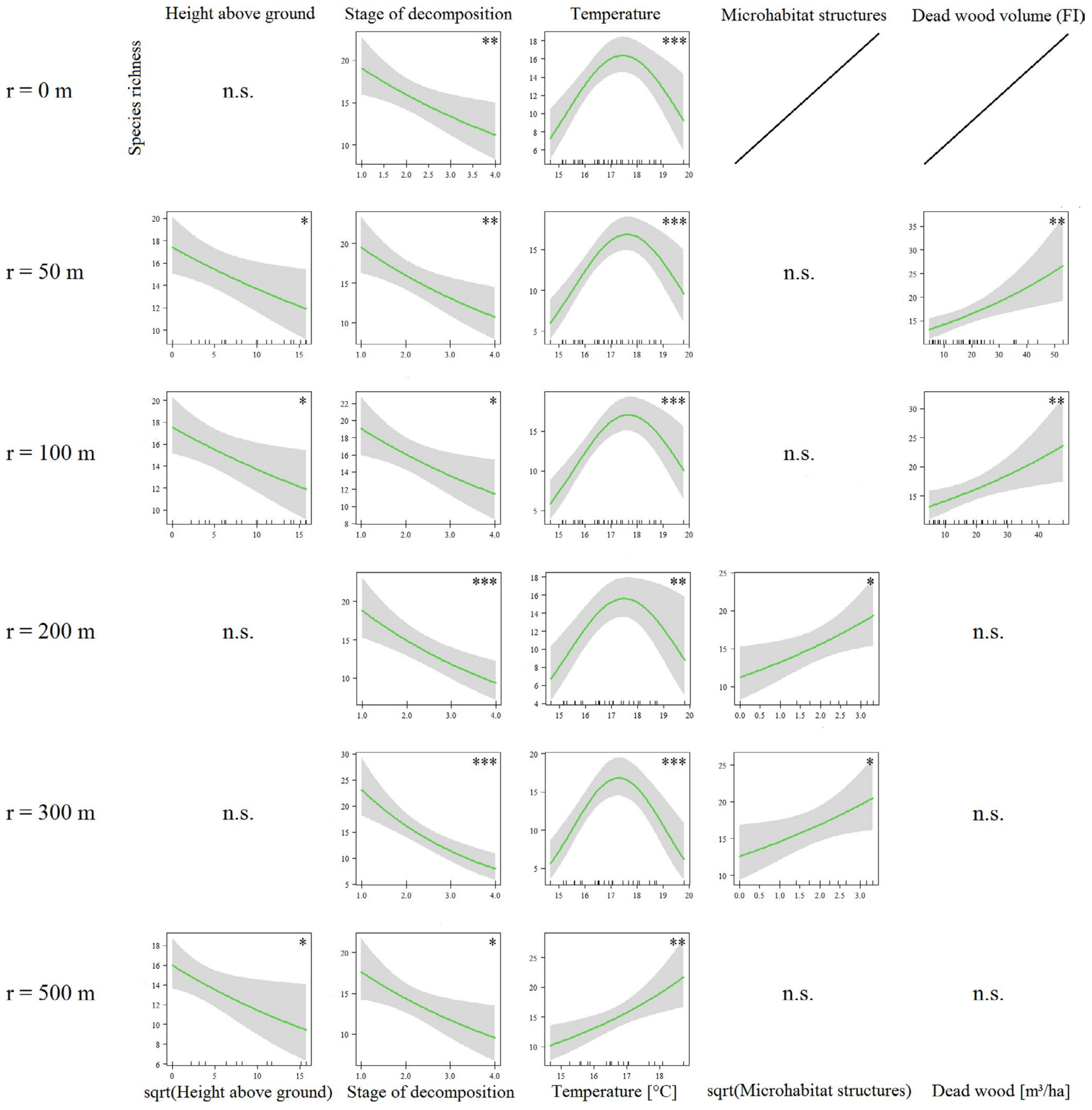

FIGURE 2 Multivariate GLMs of the Ebrach management district (2018) of different radii around the focal tree hollows ($r \le 100$ m: $n = 50$, $r = 200$ m: $n = 37$, $r = 300$ m: $n = 32$, $r = 500$ m: $n = 24$). Total species richness of saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

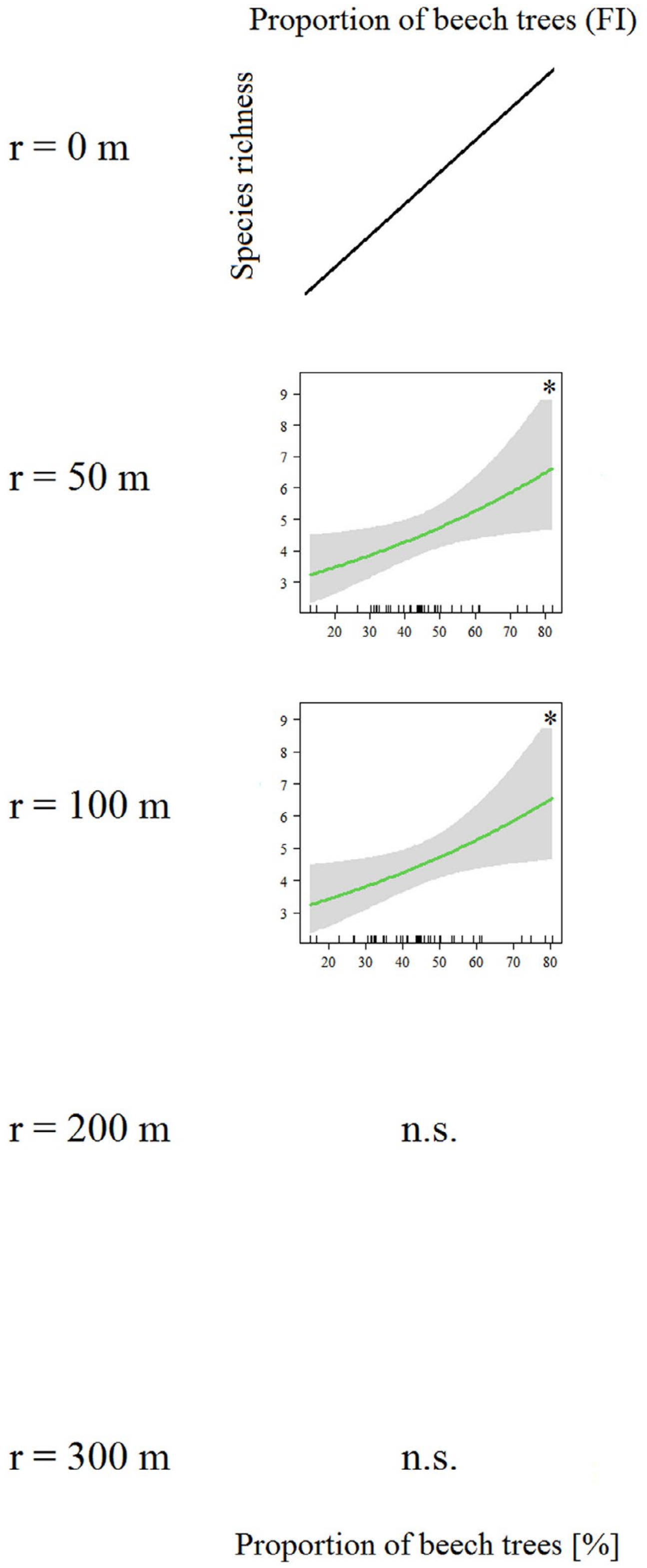

**FIGURE 3** Multivariate GLMs of the Fichtelberg management district (2018) of different radii around the focal tree hollows ($r \le 100$ m: $n = 43$, $r = 200$ m: $n = 36$, $r = 300$ m: $n = 33$, $r = 500$ m: $n = 28$). Total species richness of saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

($z = -2.23$, $p < .05$). This can be explained by a single tree hollow with a small entrance area. When that hollow was removed from the analyses, the relationship became positive. There was a negative relationship between species richness and height of the hollow entrance above ground ($z = -1.96$, $p < .05$). The number of microhabitat structures in a 30 m radius around the tree hollows

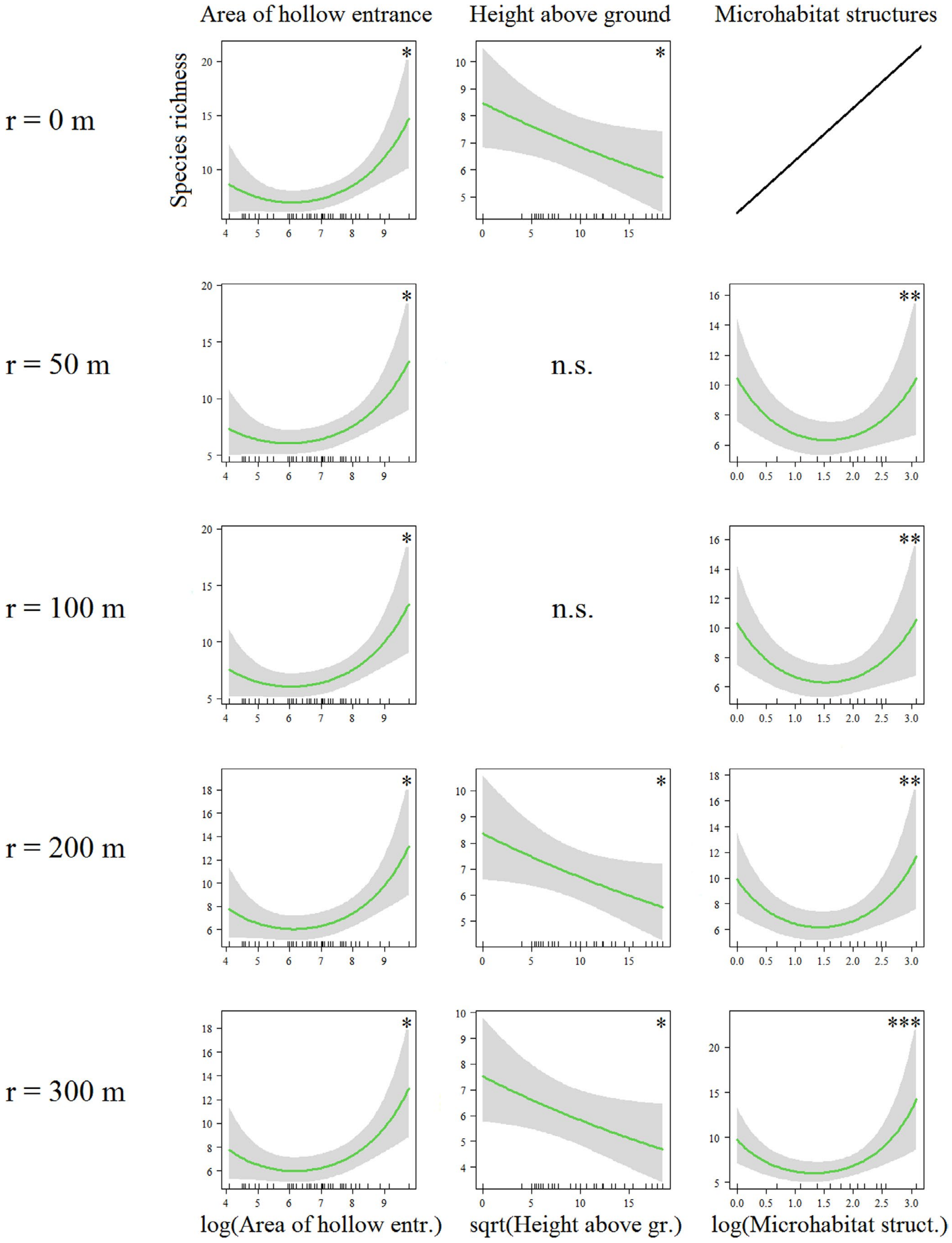

**FIGURE 4** Multivariate GLMs of the Kelheim management district (2019) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 41$, $r = 200$ m: $n = 35$, $r = 300$ m: $n = 32$). Total species richness of saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

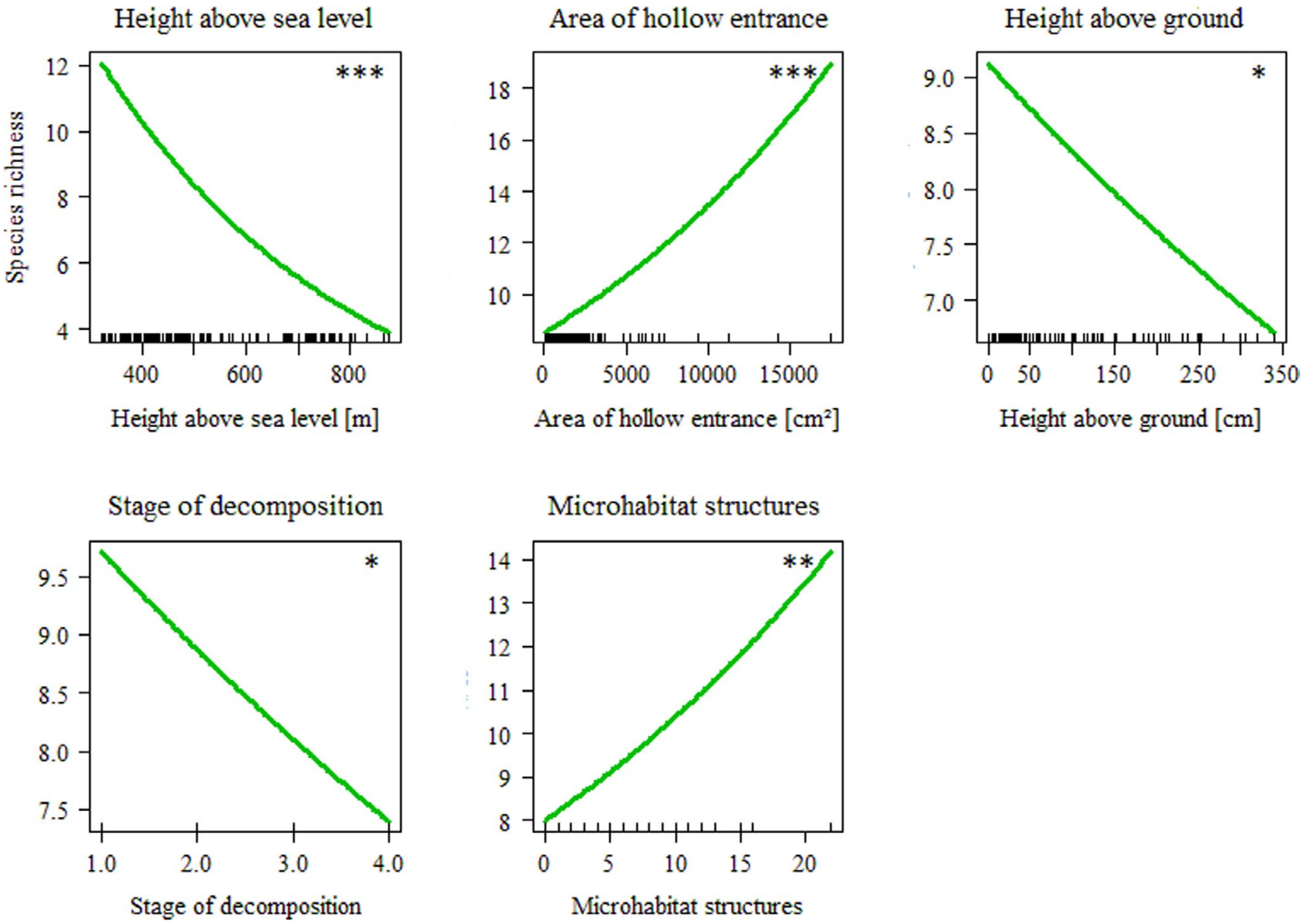

**FIGURE 5** Generalized linear mixed effects models (GLMEs) of the three forest management districts combined ($n = 134$ tree hollows). Total species richness of saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

(*surrounding microhabitat structures*, $r = 30$ m, $z = -3.16$, $p < .01$) also showed a U-shaped relationship to total species richness (Figure 4, Table A5). Pseudo-$r^2$ values that show the explanatory power of the models range from 0.240 to 0.434 depending on the radius (Table A5).

Species richness of 28 threatened saproxylic beetle species was positively related to the volume of the tree hollows ($z = 3.21$, $p < .01$), the *area of hollow entrance* ($z = 2.54$, $p < .05$) and the *temperature* inside the hollows ($z = 2.28$, $p < .05$) (Figure A9, Table A6). As there were no statistically significant parameters of forest structure, Pseudo-$r^2$ that shows the explanatory power of the models is 0.293 for all radii (Table A6).

### 3.2.4 | Combined analysis of the three forest management districts

Species richness of saproxylic beetles over all three management districts combined was negatively related to local tree hollow parameters *height above sea level* ($z = -4.45$, $p < .001$), height of the hollow entrance above ground ($z = -2.15$, $p < .05$), and the *stage of decomposition* of the wood mould ($z = -2.19$, $p < .05$), and positively related to the *area of hollow entrance* ($z = 4.17$, $p < .001$). The only parameter of forest structure that explained total species richness across all three management districts was the number of microhabitat structures in a 30 m radius around the tree hollows (*surrounding microhabitat structures*, $z = 2.70$, $p < .01$) (Figure 5, Table A7).

When only the 61 threatened saproxylic beetle species were included in the analysis, species richness was positively related to the volume of the tree hollows ($z = 2.18$, $p < .05$), and the *temperature* inside the hollows ($z = 5.37$, $p < .001$), and negatively related to *height above sea level* ($z = -5.47$, $p < .001$). The only parameter describing forest structure that explained species richness of threatened saproxylic beetles across all three management districts was again the number of microhabitat structures in a 30 m radius around the tree hollows (*surrounding microhabitat structures*, $z = 2.01$, $p < .05$) (Figure A10, Table A8).

## 4 | DISCUSSION

In this study, the influence of local tree hollow parameters as well as the surrounding forest structure within three managed forests on species richness of saproxylic beetles in tree hollows was investigated. Our results confirm the findings that species richness of hollow-using saproxylic beetles is related on the one hand to different properties of the tree hollows themselves (Micó et al., 2015; Quinto et al., 2014; Schauer et al., 2018): when all three forest regions were combined the area of hollow entrance positively influenced total species richness while height above ground and stage of decomposition negatively influenced total species richness of saproxylic beetles; on the other hand, the influence of these local properties of tree hollows on species richness of saproxylic beetles also depends on surrounding forest structure. In forest regions with a higher proportion of deciduous trees (Ebrach, Kelheim) the influence of local tree hollow parameters was more pronounced than in the mostly coniferous Fichtelberg forest region. When regions were analyzed separately, the only parameter (of those investigated) that influenced total species richness of saproxylic beetles in the conifer-dominated Fichtelberg region was the proportion of beech trees in the surrounding of focal tree hollows. Beech trees in this forest region can be described as isolated within a matrix of coniferous trees which made their presence the most important resource for saproxylic beetles under these circumstances. Therefore, the influence of local tree hollow characteristics on diversity of saproxylic beetles must be seen in relation to surrounding forest structure. However, the sample size is potentially limited for the analysis of each region separately, as there were only 41–50 tree hollows examined in each forest region.

## 4.1 | Influence of local tree hollow parameters

One local tree hollow parameter that showed a positive relationship to species richness when all three forest regions were combined was area of hollow entrance. A positive relationship with area of hollow entrance was also observed for threatened species in Kelheim. This relationship has also been observed in previous studies (Quinto et al., 2014; Ranius, 2002; Schauer et al., 2018). It has been proposed that many saproxylic species prefer a less humid microclimateand a larger hollow entrance is associated with a reduction in humidity inside the tree hollow (Schauer et al., 2018).

We also found a positive relationship between hollow volume and number of threatened species in all three forest regions combined, as well as in Ebrach and Kelheim alone. As many threatened saproxylic beetle species are assumed to have high habitat requirements concerning not only quantity but quality of dead wood structures (Müller et al., 2005), several studies have reported the association of threatened species with large tree hollows that offer a greater diversity of microhabitats (Ranius et al., 2009).

There was a negative relationship between total species richness and the stage of wood mould decomposition when all three management districts were combined as well as for Ebrach alone for all species as well as for threatened species. A similar relationship has been reported by Stokland and Siitonen (2012), who proposed that the number of saproxylic species in forest dead wood declined at later stages of decay. While we found early stages of wood mould decomposition to contain the highest species richness, both Sverdrup-Thygeson et al. (2010) and Schauer et al. (2018) reported the highest species richness in tree hollows with intermediate stages of wood mould decomposition.

In Ebrach total species richness of saproxylic beetles was related to temperature inside the tree hollows. We found the highest species richness in tree hollows with intermediate mean temperatures of 17–18°C. The positive relationship between temperature and species richness in the $r = 500$ m model can be explained by three hollows with a relatively high average temperature that contained relatively few beetle species and that were randomly removed from the $r = 500$ m model due to spatial overlap with other hollows or non-forest areas. However, for threatened species in all three forest regions combined, as well as in Kelheim alone, we observed a strictly positive relationship with temperature. Many other studies also reported a positive relationship between temperature and species richness (Müller et al., 2015; Schauer et al., 2018), especially for threatened saproxylic beetle species (Lindhe et al., 2005; Widerberg et al., 2012).

In Ebrach and Kelheim we found higher species richness in tree hollows located closer to the ground. We observed the same relationship for total species richness in all three forest regions combined as well as for threatened species in Ebrach. This has also been reported by Schauer et al. (2018) for the Ebrach management district as well as Quinto et al. (2014) in Mediterranean deciduous oak woodland. One possible explanation could be the higher number of generalist predator species in tree hollows located closer to the ground (Ranius, 2002; Ranius, Svensson, et al., 2009). It has also been reported that generalist species that can dwell on the forest floor are more dominant in tree hollows that are connected to the ground (Siitonen, 2012). However, as we only examined tree hollows up to a height of 350 cm above ground, we only cover a limited vertical range of tree hollows, which may bias results.

Total and threatened species richness for all three management districts combined was negatively related to height of the tree hollows above sea level. It has previously been shown that altitude negatively affected saproxylic beetle diversity (Johansson et al., 2017; Wu et al., 2008) as higher elevations are generally associated with colder climate. Johansson et al. (2017) described gradients in altitude as important determinants of the distribution of saproxylic beetle assemblages in boreal forests in Sweden. Similarly, Müller et al. (2015) proposed that conservationists, landscape managers, and ecologists should pay more attention to the climate gradient as one fundamental driver of saproxylic insect diversity.

## 4.2 | Influence of forest structure at larger spatial scales

Beside parameters of the tree hollows themselves, we also analyzed forest structure at different spatial scales. In contrast to tree hollow parameters, the parameters of forest structure that influenced saproxylic beetle diversity in tree hollows were mostly highly idiosyncratic with respect to region, which was most likely due to the differences in tree-species composition between regions.

It has previously been reported that the number of tree hollows in the surrounding of a focal tree hollow had a positive influence on species richness of saproxylic beetles (Ranius & Wilander, 2000; Schauer et al., 2018). In our study we could not confirm this, but the number of microhabitat structures, indicating the number of possible future tree hollows or other dead wood related structures to develop, in a 30 m radius around each focal tree hollow explained species richness of saproxylic beetles across all three forest regions as well as for Ebrach and Kelheim alone. The same result was obtained for threatened species in all three regions combined as well as for Ebrach and Fichtelberg alone.

In Ebrach, the region with the highest proportion of deciduous tree species, species richness of saproxylic beetles showed a significant positive relationship with dead wood volume at small radii of 50 and 100 m around the focal tree hollows but not at larger spatial scales. A reason for the restriction of the influence of dead wood volume to smaller spatial scales might be that dispersal abilities of most saproxylic insect species are still unknown and might be rather small (Feldhaar & Schauer, 2018). In the other two forest management districts, with fewer beech trees and a lower proportion of deciduous trees, there was no relationship between dead wood volume and species richness. The importance of dead wood for a diverse fauna of saproxylic insects in forests has been extensively described before (Floren et al., 2014; Gossner, Floren, et al., 2013; Müller et al., 2015; Similä et al., 2003). Lassauce et al. (2011) proposed that additional variables like the type of dead wood or stage of decomposition should be taken into account. Stokland and Siitonen (2012) state that the majority of saproxylic beetle species (89%) are specialized either on deciduous or on coniferous dead wood. Dead wood of mostly coniferous trees, as it prevailed in the forest management district Fichtelberg, did not promote species richness of saproxylic beetles in tree hollows in beech trees. In contrast, the only parameter that influenced total species richness of saproxylic beetles in the conifer dominated Fichtelberg management district was the proportion of beech trees in the surrounding of focal tree hollows, up to a radius of 100 m around tree hollows. This finding implies that in a forest region like the Fichtelberg management district where suitable tree hollow habitats in deciduous trees are very limited the number of potential habitat trees in the surrounding of a focal tree hollow is the most important parameter influencing saproxylic beetle diversity in tree hollows, and the quality of the habitat – the tree hollow itself – might be of secondary importance.

Implications for forest management that can be inferred from this study include the conservation of developing and existing tree hollows as each tree hollow is unique with regard to the range of microhabitats within (Quinto et al., 2014; Siitonen, 2012). This study has also shown that the number of tree-related microhabitats (e. g. woodpecker holes, injuries to the bark) in a forest stand is not only beneficial to the development of future tree hollows but seems to already increase species richness of saproxylic beetles in tree hollows and should therefore be conserved. Another important implication for forest management is the further enrichment of dead wood in managed forests (Gossner, Floren, et al., 2013; Müller et al., 2015), especially dead wood from deciduous tree species as saproxylic beetles have been shown to react sensitively not only to the amount but also the variety and distribution of dead wood (Sverdrup-Thygeson et al., 2014). Tree-species composition has also proven to greatly influence diversity of hollow-using beetles (Floren et al., 2014). Therefore, increasing the proportion of deciduous trees in managed forests with a high proportion of coniferous trees will increase species richness of saproxylic beetles in tree hollows.

## 5 | CONCLUSIONS

Local tree hollow characteristics influence the diversity of saproxylic beetles in tree hollows irrespective of region and management. Parameters of forest structure at larger spatial scales differ in their importance for saproxylic beetle species richness depending on the forest region's tree-species composition. Therefore, the influence of local tree hollow parameters on species richness of saproxylic beetles should be considered in the context of surrounding forest structure at larger spatial scales. Forest inventory data can support this process by providing necessary data without additional field work. Thus, forest inventory data can be a powerful tool, in combination with local tree hollow parameters, to assess diversity of hollow-using beetles in managed forests and help forest authorities decide which conservation measures to apply in certain parts of forest regions to effectively protect saproxylic beetles in tree hollows.

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### CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

## AUTHOR CONTRIBUTIONS

**Benjamin Henneberg:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (equal); Supervision (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Simon Bauer:** Data curation (equal); Formal analysis (equal); Investigation (equal); Writing-original draft (supporting). **Markus Birkenbach:** Data curation (equal); Formal analysis (equal); Investigation (equal); Writing-original draft (supporting). **Vanilla Mertl:** Data curation (equal); Formal analysis (equal); Investigation (equal); Writing-original draft (supporting). **Manuel J. Steinbauer:** Data curation (equal); Formal analysis (equal); Methodology (equal); Software (equal); Visualization (supporting). **Heike Feldhaar:** Conceptualization (lead); Funding acquisition (lead); Methodology (lead); Project administration (lead); Supervision (lead); Writing-original draft (supporting). **Elisabeth Obermaier:** Conceptualization (lead); Funding acquisition (lead); Methodology (lead); Project administration (lead); Supervision (lead); Writing-original draft (supporting).

## DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from Dryad digital repository: https://doi.org/10.5061/dryad.66t1g1k1q.

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## REFERENCES

Bässler, C., Ernst, R., Cadotte, M., Heibl, C., & Müller, J. (2014). Near-to-nature logging influences fungal community assembly processes in a temperate forest. *Journal of Applied Ecology*, *51*, 939–948.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

BaySF (2015). *Regionales Naturschutzkonzept für den Forstbetrieb Kelheim, Stand Mai 2015*. Bayerische Staatsforsten. https://www.baysf.de/fileadmin/user_upload/01-ueber_uns/05-standorte/FB_Kelheim/15_05_20_Endfassung_NSK_FB_Kelheim_pdf

BaySF (2017). *Naturschutzkonzept für den Forstbetrieb Fichtelberg, Stand Februar 2017*. Bayerische Staatsforsten. https://www.baysf.de/fileadmin/user_upload/01-ueber_uns/05-standorte/FB_Fichtelberg/Naturschutzkonzept_Forstbetrieb_Fichtelberg.pdf

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *R Journal*, *9*, 56.

ESRI (2018). *ArcGIS Desktop: Version 10.6*. Environmental Systems Research Institute.

Feldhaar, H., & Schauer, B. (2018). Dispersal of saproxylic insects. In M. D. Ulyshen (Ed.), *Saproxylic insects: Diversity, ecology and conservation* (pp. 515–546). Springer.

Floren, A., Muller, T., Dittrich, M., Weiss, M., & Linsenmair, K. E. (2014). The influence of tree species, stratum and forest management on beetle assemblages responding to deadwood enrichment. *Forest Ecology and Management*, *323*, 57–64.

Gossner, M. M., Floren, A., Weisser, W. W., & Linsenmair, K. E. (2013). Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. *Forest Ecology and Management*, *302*, 404–413. https://doi.org/10.1016/j.foreco.2013.03.039

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology*, *27*, 605–614. https://doi.org/10.1111/cobi.12023

Gouix, N., & Brustel, H. (2012). Emergence trap, a new method to survey *Limoniscus violaceus* (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation*, *21*, 421–436.

Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. http://CRAN.R-project.org/package=DHARMa

Jarzabek, A. (2005). *Baumhöhlen als Schlüssellebensraum für xylobionte Käfer in Buchenwäldern*. M. Sc. thesis. Fachhochschule Weihenstephan.

Johansson, T., Gibb, H., Hjältén, J., & Dynesius, M. (2017). Soil humidity, potential solar radiation and altitude affect boreal beetle assemblages in dead wood. *Biological Conservation*, *209*, 107–118.

Kleiber, C., & Zeileis, A. (2008). *Applied econometrics with R*. Springer Science & Business Media.

Köhler, F. (2000). *Totholzkäfer in Naturwaldzellen des nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung [Saproxylic Beetles in Nature Forests of the Northern Rhineland. Comparative Studies on the Saproxylic Beetles of Germany and Contributions to German Nature Forest Research]* (pp. 351). Landesamt Agrarordnung NRW. In German.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., & Winter, S. (2016). Katalog der Baummikrohabitate - Referenzliste für Feldaufnahmen. *Integrate + Technical Paper*, *13*, 16.

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachatgh, T., Micheli, A. K., Regneryjk, B., & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, *84*, 194–207.

Lassauce, A., Paillet, Y., Jactel, H., & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, *11*, 1027–1039.

Leverkus, A. B., Gustafsson, L., Lindenmayer, D. B., Castro, J., Rey Benayas, J. M., Ranius, T., & Thorn, S. (2020). Salvage logging effects on regulating ecosystem services and fuel loads. *Frontiers in Ecology and the Environment*, *18*, 391–400.

Lindenmayer, D., Laurance, W., & Franklin, J. (2012). Global decline in large old trees. *Science*, *338*, 1305–1306.

Lindhe, A., Lindelöw, Å., & Åsenblad, N. (2005). Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation*, *14*, 3033–3053.

Micó, E. (2018). Saproxylic insects in tree hollows. In M. D. Ulyshen (Ed.), *Saproxylic insects: Diversity, ecology and conservation* (pp. 693–727). Springer.

Micó, E., García-López, A., Brustel, H., Padilla, A., & Galante, E. (2013). Explaining the saproxylic beetle diversity of a protected Mediterranean area. *Biodiversity and Conservation*, *22*, 889–904.

Micó, E., García-López, A., Sánchez, A., Juárez, M., & Galante, E. (2015). What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? *Journal of Insect Conservation*, *19*, 141–153. https://doi.org/10.1007/s10841-015-9754-9

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M. M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., & Gossner, M. M. (2015). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography*, *38*, 499–509.

Müller, J., Bußler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J., & Zabransky, P. (2005).

Urwald relict species - saproxylic beetles indicating structural qualities and habitat tradition. *Waldökologie Online*, *2*, 106–113.

Müller, J., Bußler, H., & Kneib, T. (2008). Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation*, *12*, 107.

Müller, J., Jarzabek-Müller, A., Bussler, H., & Gossner, M. M. (2014). Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation*, *17*, 154–162.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2013). *vegan: Community ecology package*. R package version 2.5-6. http://CRAN.R-project.org/package=vegan

Quinto, J., Micó, E., Martínez-Falcón, A. P., Galante, E., & de los Angeles Marcos-Garcia, M. (2014). Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *Journal of Insect Conservation*, *18*, 981–992.

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Ranius, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation*, *103*, 85–91.

Ranius, T., Johansson, V., Schroeder, M., & Caruso, A. (2015). Relative importance of habitat characteristics at multiple spatial scales for wood-dependent beetles in boreal forest. *Landscape Ecology*, *30*, 1931–1942.

Ranius, T., Niklasson, M., & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management*, *257*, 303–310. https://doi.org/10.1016/j.foreco.2008.09.007

Ranius, T., Svensson, G. P., Berg, N., Niklasson, M., & Larsson, M. C. (2009). The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Annales Zoologici Fennici*, *46*, 205–216.

Ranius, T., & Wilander, P. (2000). Occurrence of *Larca lata* HJ Hansen (Pseudoscorpionida: Garypidae) and *Allochernes wideri* CL Koch (Pseudoscorpionida: Chernetidae) in tree hollows in relation to habitat quality and density. *Journal of Insect Conservation*, *4*, 23–31.

Schauer, B., Steinbauer, M. J., Vailshery, L. S., Müller, J., Feldhaar, H., & Obermaier, E. (2018). Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation*, *27*, 853–869.

Schmidl, J., & Büche, B. (2018). Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick (Stand Sept. 2011). *Naturschutz und Biologische Vielfalt*, *70* (in preparation).

Schmidl, J., & Bußler, H. (2004). Ecological guilds of xylobiontic (saproxylic) beetles in Germany and their use in landscape ecological surveys. *Naturschutz und Landschaftsplanung*, *36*, 202–218.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D., & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, *53*, 934–943.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., & Müller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, *29*, 382–390.

Seibold, S., Gossner, M. M., Simons, N., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*, 671–674.

Seibold, S., & Thorn, S. (2018). The importance of dead-wood amount for saproxylic insects and how it interacts with dead-wood diversity and other habitat factors. In M. D. Ulyshen (Ed.), *Saproxylic insects* (pp. 607–637). Springer.

Siitonen, J. (2012). Microhabitats. In J. N. Stokland, B. G. Jonsson, & J. Siitonen (Eds.), *Biodiversity in dead wood* (pp. 150–182). Cambridge University Press.

Similä, M., Kouki, J., & Martikainen, P. (2003). Saproxylic beetles in managed and seminatural Scots pine forests: Quality of dead wood matters. *Forest Ecology and Management*, *174*, 365–381.

Speight, M. C. (1989). *Saproxylic invertebrates and their conservation*. Council of Europe.

Stokland, J. N., & Siitonen, J. (2012). Mortality factors and decay succession. In J. N. Stokland, B. G. Jonsson, & J. Siitonen (Eds.), *Biodiversity in dead wood* (pp. 110–149). Cambridge University Press.

Sverdrup-Thygeson, A., Gustafsson, L., & Kouki, J. (2014). Spatial and temporal scales relevant for conservation of dead-wood associated species: Current status and perspectives. *Biodiversity and Conservation*, *23*, 513–535.

Sverdrup-Thygeson, A., Skarpaas, O., & Ødegaard, F. (2010). Hollow oaks and beetle conservation: The significance of the surroundings. *Biodiversity and Conservation*, *19*, 837–852.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., & Müller, J. (2016). Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecology Letters*, *19*, 163–170.

Thorn, S., Seibold, S., Leverkus, A. B., Michler, T., Müller, J., Noss, R. F., Stork, N., Vogel, S., & Lindenmayer, D. B. (2020). The living dead: Acknowledging life after tree death to stop forest degradation. *Frontiers in Ecology and the Environment*, *18*, 505–512.

Vítková, L., Bače, R., Kjučukov, P., & Svoboda, M. (2018). Deadwood management in Central European forests: Key considerations for practical implementation. *Forest Ecology and Management*, *429*, 394–405.

Vogel, S., Gossner, M. M., Mergner, U., Müller, J., & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. *Journal of Applied Ecology*, *57*, 2075–2085.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, *65*, 457–480.

Widerberg, M. K., Ranius, T., Drobyshev, I., Nilsson, U., & Lindbladh, M. (2012). Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodiversity and Conservation*, *21*, 3035–3059.

Wu, J., Yu, X. D., & Zhou, H. Z. (2008). The saproxylic beetle assemblage associated with different host trees in Southwest China. *Insect Science*, *15*, 251–261.

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## APPENDIX A

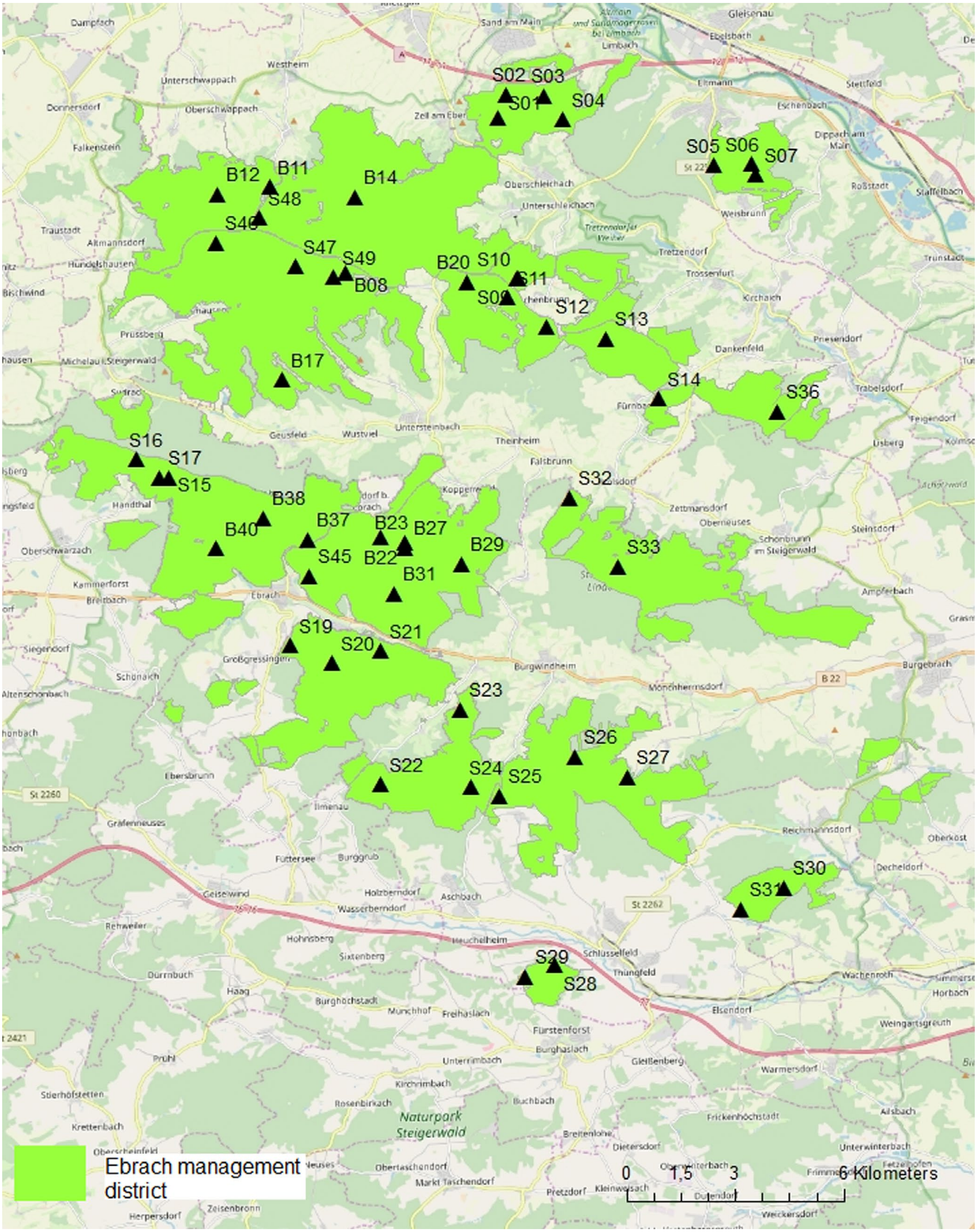

FIGURE A1 Examined tree hollows in the Ebrach forest management district ($n = 50$)

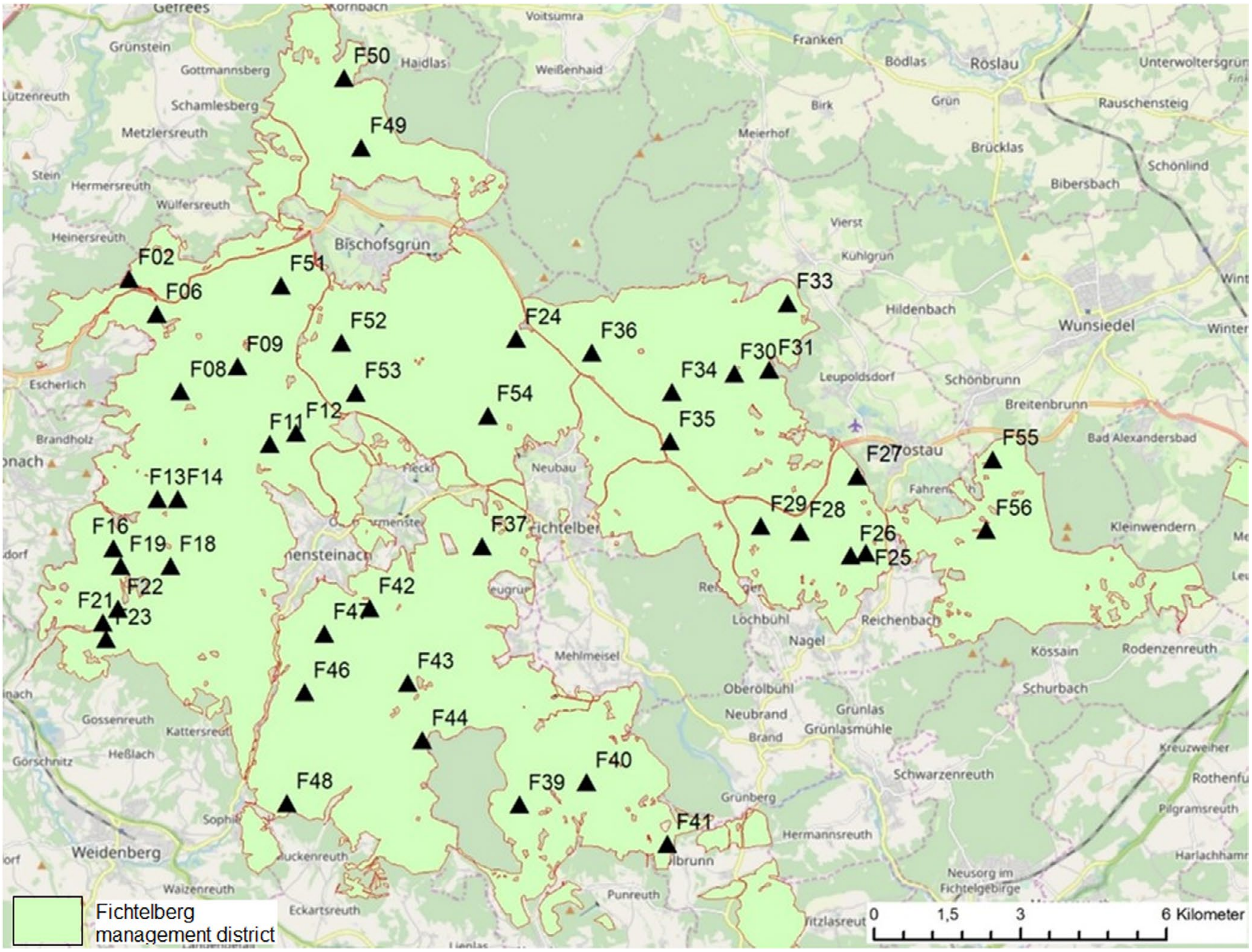

**FIGURE A2** Examined tree hollows in the Fichtelberg forest management district ($n = 43$)

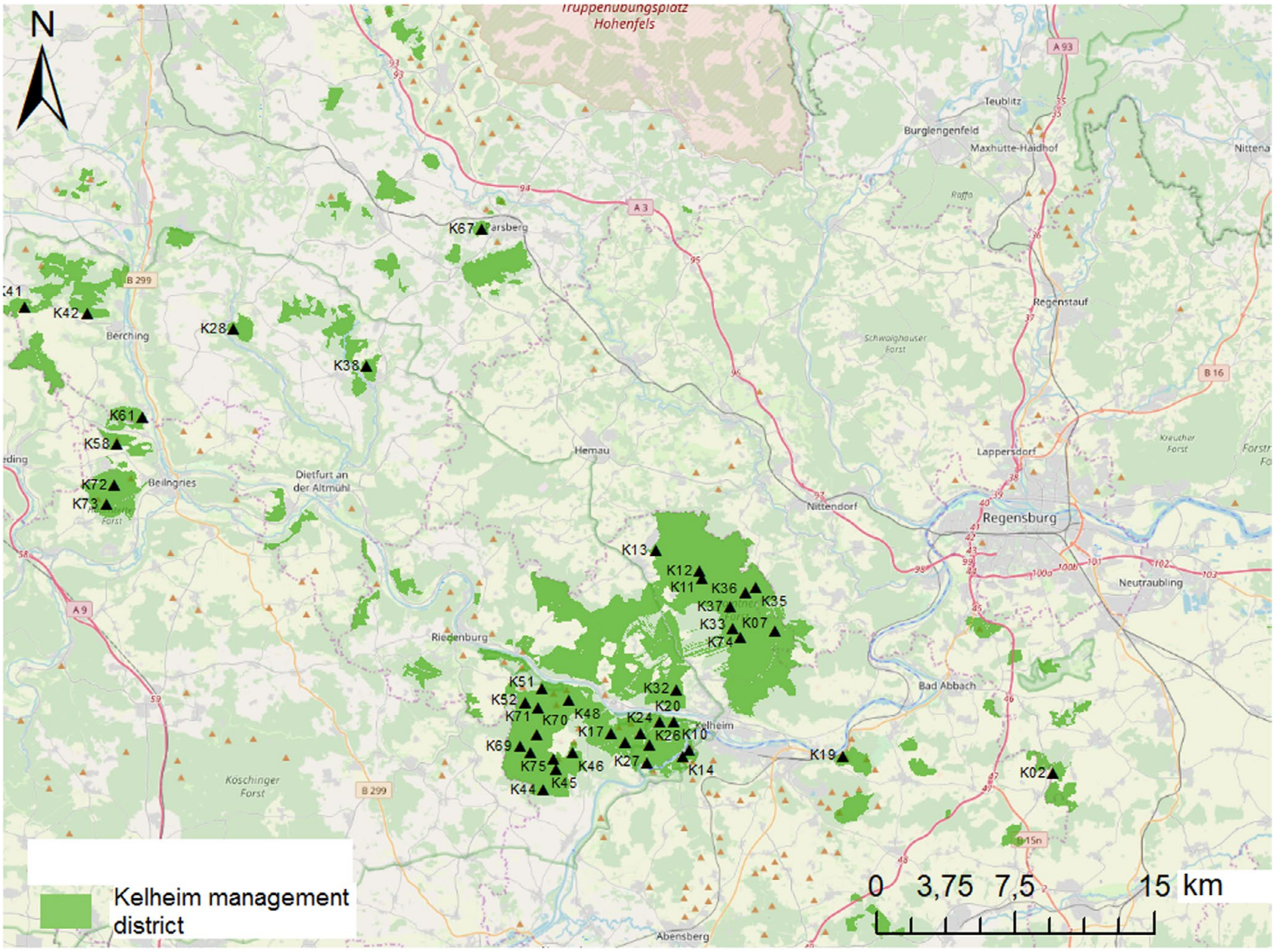

FIGURE A3 Examined tree hollows in the Kelheim forest management district ($n = 41$)

**FIGURE A4** Emergence trap (modified from Gouix & Brustel, 2012)

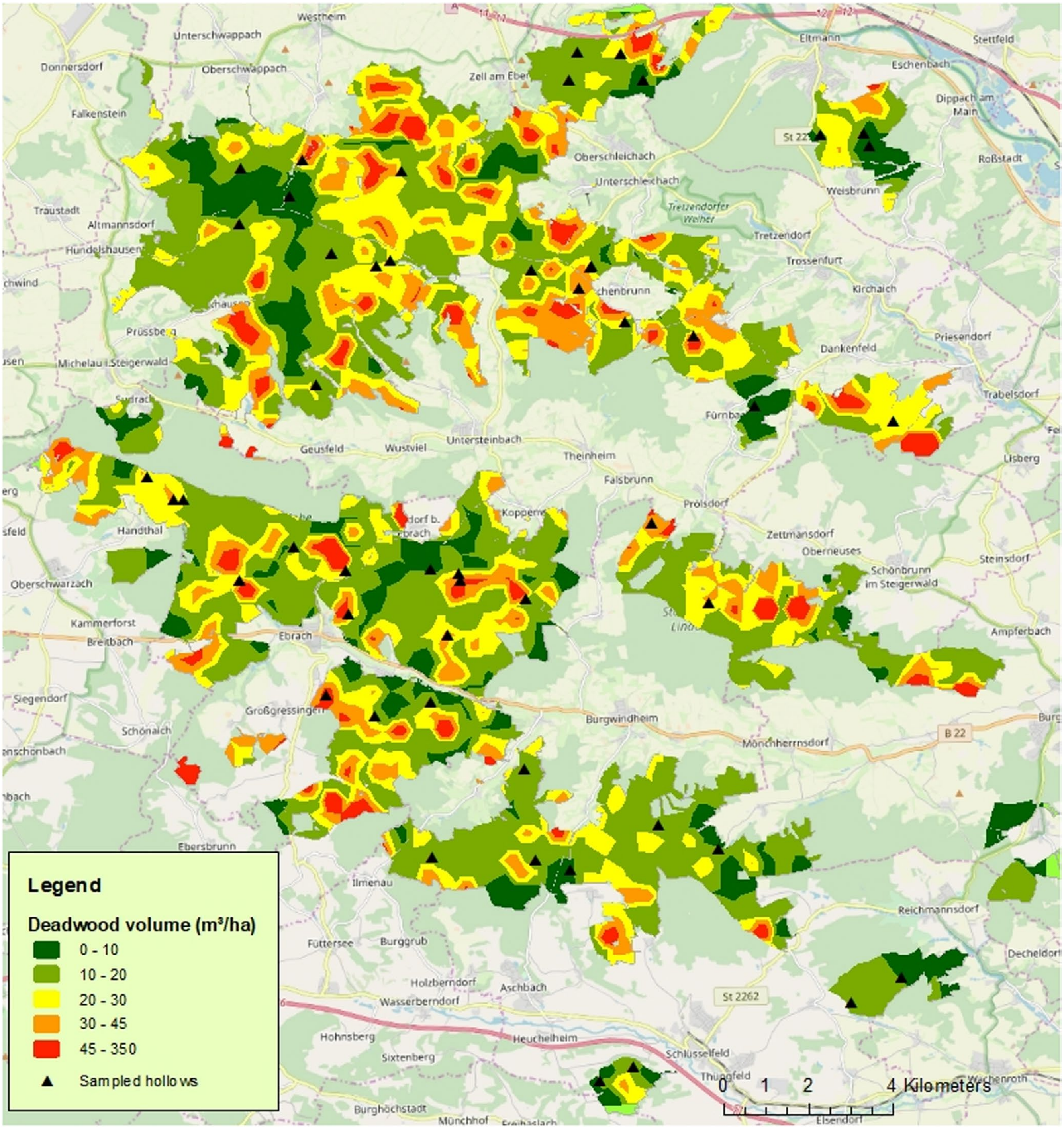

FIGURE A5 Distribution of dead wood in the Ebrach forest management district; map generated from forest inventory data using the deterministic inverse distance weighting (IDW) method

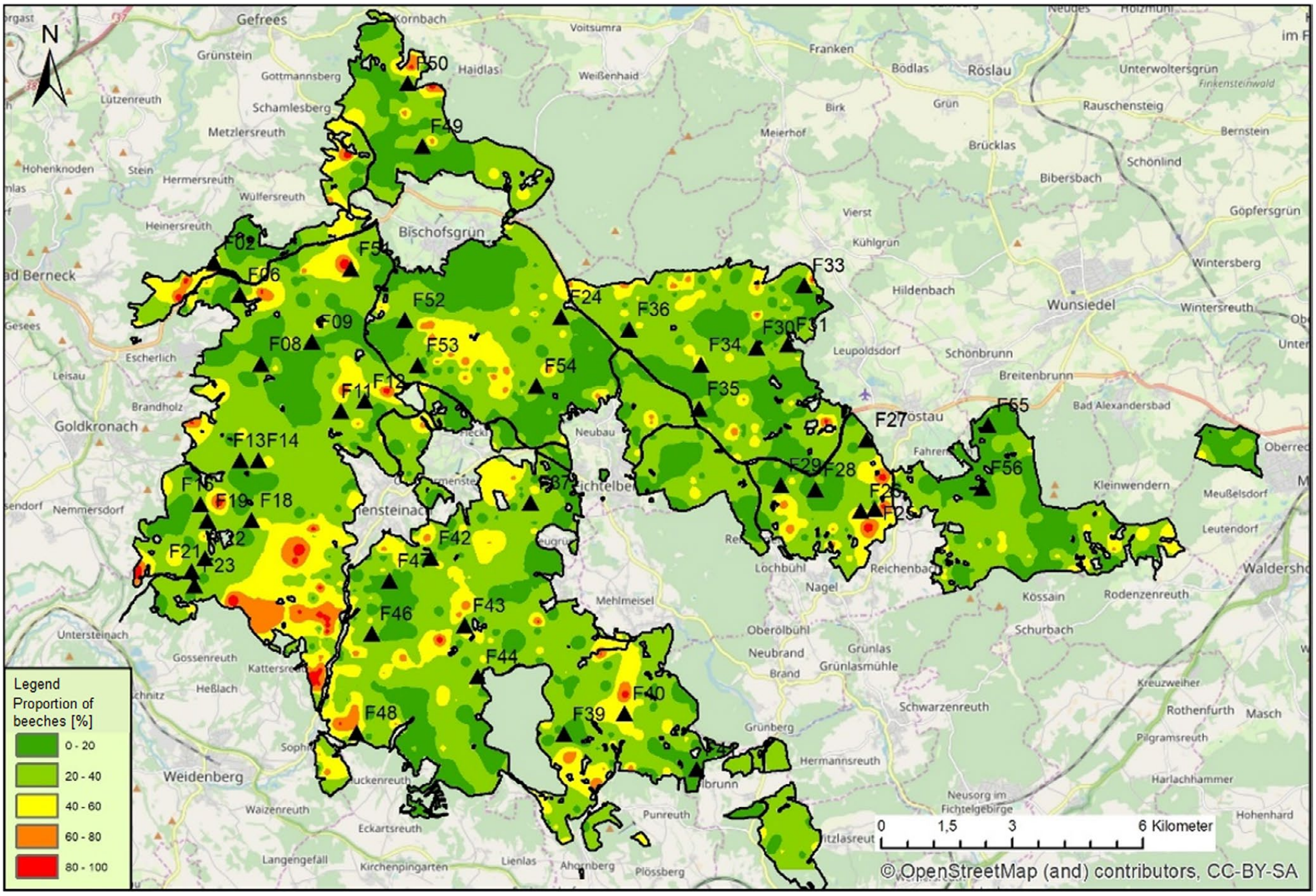

FIGURE A6 Proportion of beech trees in the Fichtelberg forest management district; map generated from forest inventory data using the deterministic inverse distance weighting (IDW) method

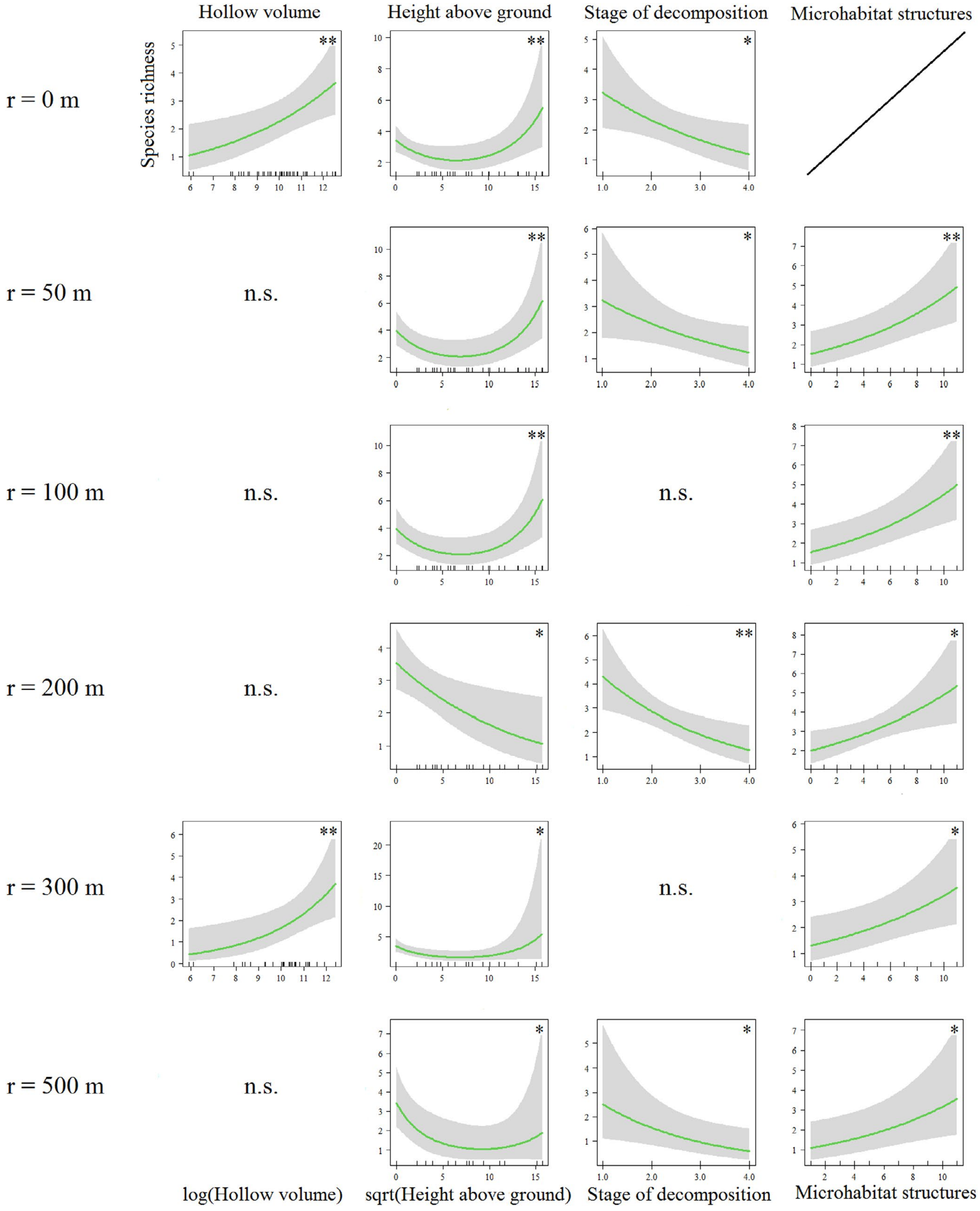

**FIGURE A7** Multivariate GLMs of the Ebrach management district (2018) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 50$, $r = 200$ m: $n = 37$, $r = 300$ m: $n = 32$, $r = 500$ m: $n = 24$). Species richness of threatened saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

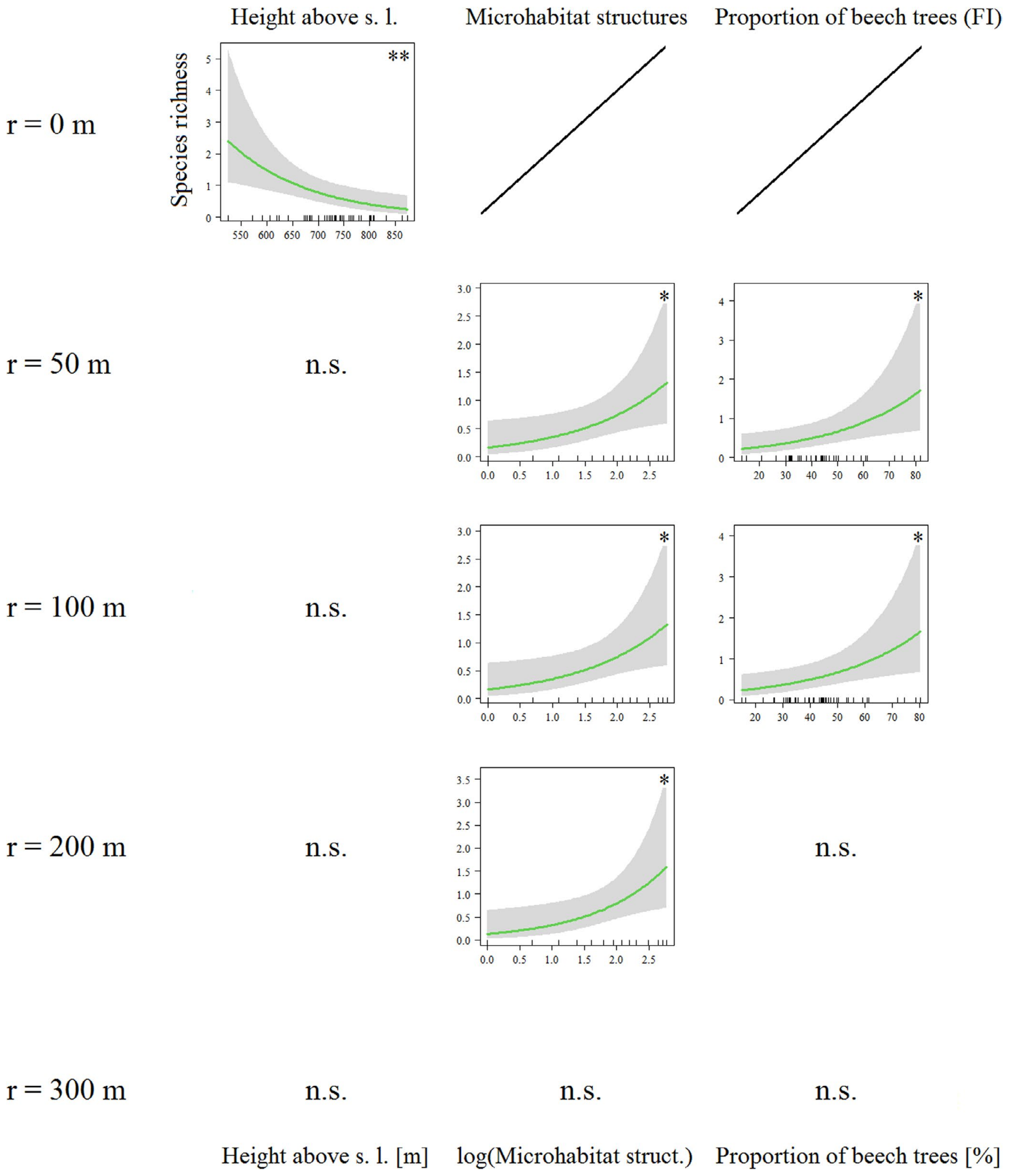

**FIGURE A8** Multivariate GLMs of the Fichtelberg management district (2018) of different radii around the focal tree hollows ($r \le 100$ m: $n = 43$, $r = 200$ m: $n = 36$, $r = 300$ m: $n = 33$, $r = 500$ m: $n = 28$). Species richness of threatened saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

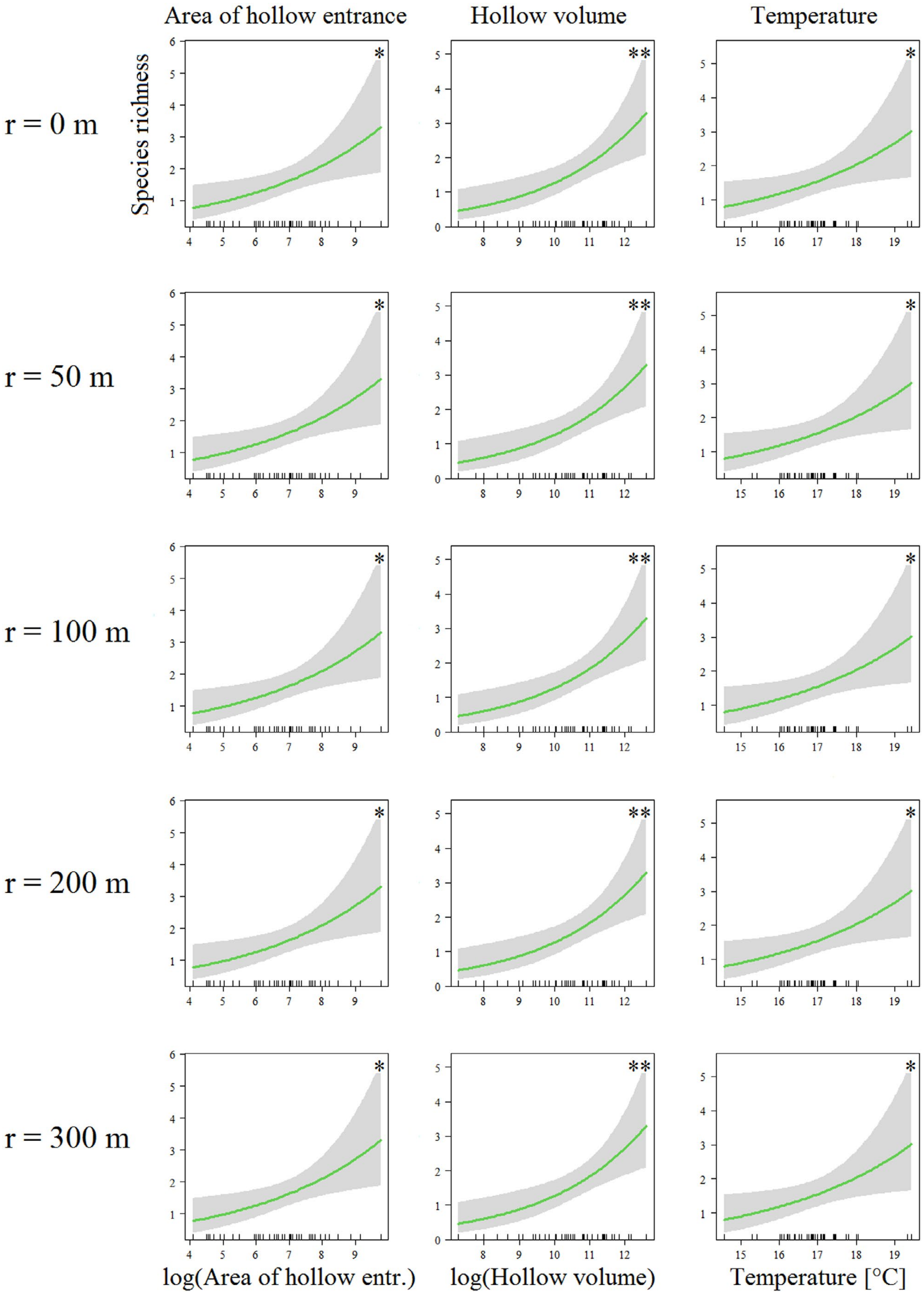
Area of hollow entrance
Hollow volume
Temperature
Species richness
r = 0 m
r = 50 m
r = 100 m
r = 200 m
r = 300 m
*
**
*
0
1
2
3
4
5
6
4
5
6
7
8
9
10
11
12
15
16
17
18
19
log(Area of hollow entr.)
log(Hollow volume)
Temperature [°C]

**FIGURE A9** Multivariate GLMs of the Kelheim management district (2019) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 41$, $r = 200$ m: $n = 35$, $r = 300$ m: $n = 32$). Species richness of threatened saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

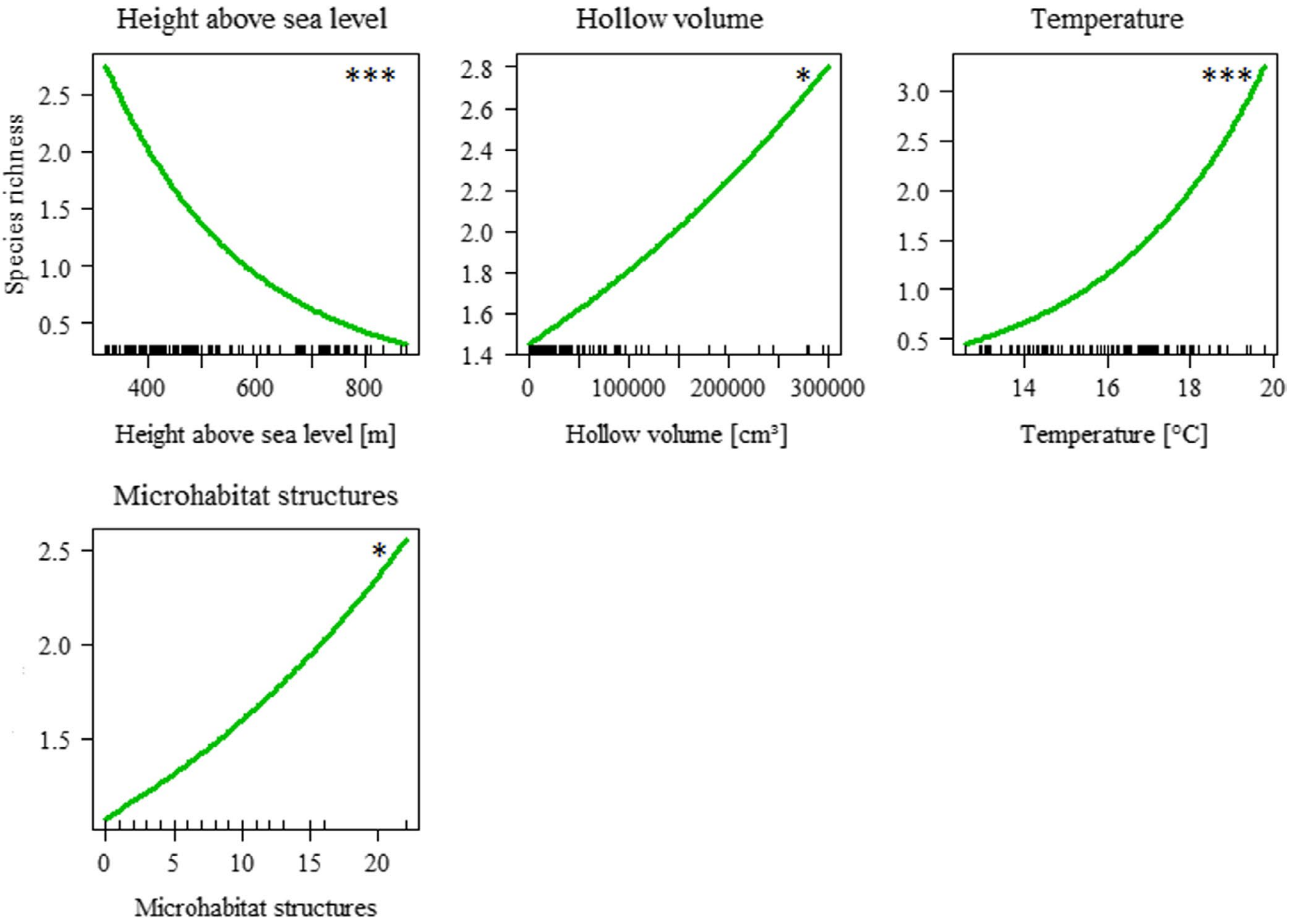

**FIGURE A10** Generalized linear mixed effects models (GLMEs) of the three forest management districts combined ($n = 134$ tree hollows). Species richness of threatened saproxylic beetles as the dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***)

**TABLE A1** Multivariate GLMs of the Ebrach management district (2018) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 50$, $r = 200$ m: $n = 37$, $r = 300$ m: $n = 32$, $r = 500$ m: $n = 24$)

| GLM/radius | Height above ground | | Stage of decomposition | | Temperature | | Microhabitat structures | | Dead wood volume (FI) | | Pseudo-$R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $r = 0$ m | n. s. | | $p = .006^{**}$ | $z = -2.746$ | $p = .001^{**}$ | $z = 3.220$ | n. a. | | n. a. | | .378 |
| $r = 50$ m | $p = .021^{*}$ | $z = -2.313$ | $p = .005^{**}$ | $z = -2.824$ | $p = .0001^{***}$ | $z = 3.821$ | n. s. | | $p = .001^{**}$ | $z = 3.238$ | .507 |
| $r = 100$ m | $p = .019^{*}$ | $z = -2.343$ | $p = .014^{*}$ | $z = -2.446$ | $p = .0001^{***}$ | $z = 3.799$ | n. s. | | $p = .007^{**}$ | $z = 2.717$ | .480 |
| $r = 200$ m | n. s. | | $p = .0003^{***}$ | $z = -3.584$ | $p = .002^{**}$ | $z = 3.162$ | $p = .021^{*}$ | $z = 2.317$ | n. s. | | .457 |
| $r = 300$ m | n. s. | | $p = 9.86\text{e}{-}06^{***}$ | $z = -4.420$ | $p = 2.91\text{e}{-}05^{***}$ | $z = 4.180$ | $p = .033^{*}$ | $z = 2.136$ | n. s. | | .595 |
| $r = 500$ m | $p = .030^{*}$ | $z = -2.165$ | $p = .015^{*}$ | $z = -2.435$ | $p = .003^{**}$ | $z = 3.003$ | n. s. | | n. s. | | .740 |

*Note:* Total species richness of saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A2** Multivariate GLMs of the Ebrach management district (2018) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 50$, $r = 200$ m: $n = 37$, $r = 300$ m: $n = 32$, $r = 500$ m: $n = 24$)

| GLM/radius | Hollow volume | | Height above ground | | Stage of decomposition | | Microhabitat structures | | Pseudo-$R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $r = 0$ m | $p = .008^{**}$ | $z = 2.648$ | $p = .017^{*}$ | $z = -2.383$ | $p = .028^{*}$ | $z = -2.198$ | n. a. | | .288 |
| $r = 50$ m | n. s. | | $p = .003^{**}$ | $z = -2.989$ | $p = .048^{*}$ | $z = -1.980$ | $p = .001^{**}$ | $z = 3.214$ | .438 |
| $r = 100$ m | n. s. | | $p = .004^{**}$ | $z = -2.918$ | n. s. | | $p = .001^{**}$ | $z = 3.248$ | .443 |
| $r = 200$ m | n. s. | | $p = .015^{*}$ | $z = -2.441$ | $p = .005^{**}$ | $z = -2.780$ | $p = .011^{*}$ | $z = 2.554$ | .386 |
| $r = 300$ m | $p = .009^{**}$ | $z = 2.577$ | $p = .011^{*}$ | $z = -2.541$ | n. s. | | $p = .015^{*}$ | $z = 2.428$ | .496 |
| $r = 500$ m | n. s. | | $p = .014^{*}$ | $z = -2.468$ | $p = .026^{*}$ | $z = -2.234$ | $p = .019^{*}$ | $z = 2.349$ | .691 |

*Note:* Species richness of threatened saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A3** Multivariate GLMs of the Fichtelberg management district (2018) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 43$, $r = 200$ m: $n = 36$, $r = 300$ m: $n = 33$, $r = 500$ m: $n = 28$)

| GLM/radius | Proportion of beech trees (FI) | | Pseudo-$R^2$ |
|---|---|---|---|
| $r = 0$ m | n. a. | | |
| $r = 50$ m | $p = .023$* | $z = 2.269$ | .113 |
| $r = 100$ m | $p = .023$* | $z = 2.280$ | .116 |
| $r = 200$ m | n. s. | | |
| $r = 300$ m | n. s. | | |

*Note:* Total species richness of saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A4** Multivariate GLMs of the Fichtelberg management district (2018) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 43$, $r = 200$ m: $n = 36$, $r = 300$ m: $n = 33$, $r = 500$ m: $n = 28$)

| GLM/radius | Height above sea level | | Microhabitat structures | | Proportion of beech trees (FI) | | Pseudo-$R^2$ |
|---|---|---|---|---|---|---|---|
| $r = 0$ m | $p = .004$** | $z = -2.889$ | n. a. | | n. a. | | .287 |
| $r = 50$ m | n. s. | | $p = .028$* | $z = 2.196$ | $p = .011$* | $z = 2.540$ | .487 |
| $r = 100$ m | n. s. | | $p = .027$* | $z = 2.211$ | $p = .012$* | $z = 2.501$ | .483 |
| $r = 200$ m | n. s. | | $p = .021$* | $z = 2.306$ | n. s. | | .304 |
| $r = 300$ m | n. s. | | n. s. | | n. s. | | .203 |

*Note:* Species richness of threatened saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A5** Multivariate GLMs of the Kelheim management district (2019) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 41$, $r = 200$ m: $n = 35$, $r = 300$ m: $n = 32$)

| GLM/radius | Area of hollow entrance | | Height above ground | | Microhabitat structures | | Pseudo-$R^2$ |
|---|---|---|---|---|---|---|---|
| $r = 0$ m | $p = .034$* | $z = -2.121$ | $p = .042$* | $z = -2.035$ | n. a. | | .240 |
| $r = 50$ m | $p = .049$* | $z = -1.968$ | n. s. | | $p = .002$** | $z = -3.155$ | .434 |
| $r = 100$ m | $p = .035$* | $z = -2.105$ | n. s. | | $p = .002$** | $z = -3.145$ | .427 |
| $r = 200$ m | $p = .026$* | $z = -2.225$ | $p = .050$* | $z = -1.963$ | $p = .001$** | $z = -3.190$ | .388 |
| $r = 300$ m | $p = .024$* | $z = -2.255$ | $p = .047$* | $z = -1.985$ | $p = .0007$*** | $z = -3.408$ | .424 |

*Note:* Total species richness of saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A6** Multivariate GLMs of the Kelheim management district (2019) of different radii around the focal tree hollows ($r \leq 100$ m: $n = 41$, $r = 200$ m: $n = 35$, $r = 300$ m: $n = 32$)

| GLM/radius | Area of hollow entrance | | Hollow volume | | Temperature | | Pseudo-$R^2$ |
|---|---|---|---|---|---|---|---|
| $r = 0$ m | $p = .011$* | $z = 2.542$ | $p = .001$** | $z = 3.210$ | $p = .022$* | $z = 2.287$ | .293 |
| $r = 50$ m | $p = .011$* | $z = 2.542$ | $p = .001$** | $z = 3.210$ | $p = .022$* | $z = 2.287$ | .293 |
| $r = 100$ m | $p = .011$* | $z = 2.542$ | $p = .001$** | $z = 3.210$ | $p = .022$* | $z = 2.287$ | .293 |
| $r = 200$ m | $p = .011$* | $z = 2.542$ | $p = .001$** | $z = 3.210$ | $p = .022$* | $z = 2.287$ | .293 |
| $r = 300$ m | $p = .011$* | $z = 2.542$ | $p = .001$** | $z = 3.210$ | $p = .022$* | $z = 2.287$ | .293 |

*Note:* Species richness of threatened saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A7** Generalized linear mixed-effects models (GLMEs) of the three forest management districts combined ($n$ = 134 tree hollows)

| | Random factor: Ebrach | Random factor: Fichtelberg | Random factor: Kelheim | Height above sea level | |
|---|---|---|---|---|---|
| GLME total spp. | Estimate = 0.187 | Estimate = −0.104 | Estimate = −0.080 | $p$ = 8.41e−06*** | $z$ = −4.454 |

*Note:* Total species richness of saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

**TABLE A8** Generalized linear mixed-effects models (GLMEs) of the three forest management districts combined ($n$ = 134 tree hollows)

| | Random factor: Ebrach | Random factor: Fichtelberg | Random factor: Kelheim |
|---|---|---|---|
| GLME threatened spp. | Estimate = 2.741e−16 | Estimate = −1.844e−16 | Estimate = −8.970e−17 |

*Note:* Species richness of threatened saproxylic beetles as dependent variable; $p < .05$ (*), $p < .01$ (**), $p < .001$ (***).

Abbreviations: n. a., not available; n. s., not significant.

| **Area of hollow entrance** | | **Height above ground** | | **Stage of decomposition** | | **Microhabitat structures** | |
|---|---|---|---|---|---|---|---|
| $p = 3.08\text{e}{-}05^{***}$ | $z = 4.168$ | $p = .032^{*}$ | $z = -2.145$ | $p = .028^{*}$ | $z = -2.193$ | $p = .007^{**}$ | $z = 2.701$ |

| **Height above sea level** | | **Hollow volume** | | **Temperature** | | **Microhabitat structures** | |
|---|---|---|---|---|---|---|---|
| $p = 4.61\text{e}{-}08^{***}$ | $z = -5.466$ | $p = .029^{*}$ | $z = 2.180$ | $p = 7.99\text{e}{-}08^{***}$ | $z = 5.367$ | $p = .045^{*}$ | $z = 2.007$ |

**Manuscript 2:**

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BH, EO, HF and SF conceived the ideas and designed the methodology (SF contributed the methodology regarding CORINE satellite data). BH collected the data. BH and BS analyzed the data. BH, HF and EO interpreted and discussed results. Figures and tables were created by BH. BH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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ORIGINAL RESEARCH

# Threatened saproxylic beetle species in tree hollows react more sensitively to surrounding landscape composition in central European managed forests than total species richness

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## Abstract

Veteran deciduous trees are a rare element in today's central European managed forests due to intensive forest management over the last 200 years, resulting in a loss of dead wood habitats like tree hollows. Saproxylic beetle species depend on dead wood, and habitat specialists, such as species relying on tree hollows, are largely threatened. To better understand how to protect saproxylic beetle assemblages in tree hollows at a landscape scale we collected beetles from tree hollows in three forest regions in Bavaria (Germany) using emergence traps. We related landscape composition at spatial scales of 300–5000 m around the tree hollows to beetle diversity in the hollows using CORINE satellite data. We also modelled four dispersal-associated morphological traits as well as functional diversity indices of the beetles in relation to landscape composition. The proportion of deciduous forest surrounding the tree hollows had positive effects on species richness of saproxylic beetles in two of the three study regions. Positive effects on threatened species were more pronounced than effects on total species richness at all spatial scales. Relationships between functional diversity and landscape composition only partly confirmed our expectations regarding better dispersal ability of beetles in isolated habitat patches. Morphological traits of saproxylic beetles did not yield any significant results. Our study indicates that threatened saproxylic beetles react more sensitively to landscape compositional changes than common species. In the light of ongoing habitat fragmentation, efforts to protect threatened saproxylic beetle species should not only include single forest stands but focus on a landscape scale and support connectivity of forest patches.

**Keywords** Saproxylic insects · Insect diversity · Insect ecology · Spatial scales

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Extended author information available on the last page of the article

## Introduction

Hollow deciduous trees are keystone structures hosting a high arthropod diversity but have been declining in numbers in central European managed forests for decades due to intensive forest management (Wetherbee et al. 2020). Modern forestry has substantially changed the tree species- and age-compositions of central European forest fragments over the last 200 years from old-growth deciduous beech- and oak-forests to younger conifer-dominated forests (Gossner et al. 2013; Seibold et al. 2015) and dramatically reduced the number of veteran deciduous trees (Lindenmayer et al. 2012; Müller et al. 2014; Sverdrup-Thygeson et al. 2017), resulting in a loss of dead wood habitats like tree hollows (Thorn et al. 2020). The formation of tree hollows most likely takes place in veteran deciduous trees where they can persist for several hundred years (Siitonen 2012). Ranius et al. (2009a) showed that 50% of oak trees (*Quercus robur*) in southern Sweden that were 200–300 years old had hollows, while oak trees that were less than 100 years old rarely had hollows (less than 1%). Tree hollows are created when mechanical damage causes injuries of the tree bark and heart-rot fungi access the wood (Siitonen 2012; Micó 2018).

Saproxylic beetles, i.e., those depending on dead wood or organisms living in dead wood for at least one part of their life cycle (Speight 1989), are important for ecosystem functioning in forest ecosystems as they promote wood decomposition through mutualistic relationships with fungi and microorganisms (Stokland et al. 2012; Ulyshen 2016), which drives element cycling and productivity (Gossner et al. 2013). However, due to the loss of dead wood habitats in central European forests, many saproxylic beetle species are endangered or have already gone extinct (Seibold et al. 2015; Thorn et al. 2020). Saproxylic beetle species that are specialized on a certain dead wood habitat such as tree hollows are exceptionally threatened, with about 75% of tree-hollow specialist species being listed in the Red List of Germany (Schmidl and Büche 2018).

To effectively protect saproxylic beetles in tree hollows, it is needed to not only acknowledge the beetles' habitat requirements at local scales (see Ranius et al. 2009b; Koch Widerberg et al. 2012; Quinto et al. 2014; Micó et al. 2015; Micó 2018; Schauer et al. 2018b; Henneberg et al. 2021), but also how landscape composition at larger spatial scales influences saproxylic beetle assemblages in tree hollows (Franc et al. 2007; Müller and Gossner 2010; Ranius et al. 2015). Landscape composition is considered a key factor explaining species richness patterns at different spatial scales (Tscharntke et al. 2012; Gonthier et al. 2014). Habitat availability at landscape scale has been shown to be of high importance for species assemblages in old trees (Sverdrup-Thygeson et al. 2014). Some studies have emphasized the importance of the surrounding landscape for local saproxylic beetle species richness (Økland et al. 1996; Franc et al. 2007). In a study from southern Sweden, Götmark et al. (2011) found that local dead wood amount was the main predictor of total species richness of saproxylic beetles in dead oak trees. In contrast, the availability of woodland habitats at landscape scale was the main predictor of species richness of threatened saproxylic beetle species (Götmark et al. 2011). Similarly, Ranius et al. (2011) also surveyed saproxylic beetles in oaks in southern Sweden and found that the occurrence of threatened species was positively affected by large-scale occurrence of oaks, indicating that they needed conservation efforts at larger spatial scales than common species. However, we still have limited knowledge of the relationship between saproxylic beetle diversity in forests and landscape factors at different spatial scales (Sverdrup-Thygeson et al. 2014), even though understanding scale dependency is crucial for the management of natural resources and conservation of biodiversity (Müller and Gossner 2010; Tscharntke et al. 2012; Micó et al. 2013; Ranius et al. 2015).

Besides the loss of dead wood habitats in central European forests, fragmentation of forest regions has been identified as another major driver of the decline of saproxylic beetle diversity (Ranius 2002; Brunet and Isacsson 2009; Lachat and Müller 2018). Since medieval times, forest areas in central Europe have decreased greatly, resulting in a fragmented mosaic of unconnected forest patches of different sizes and distributions (Rüther and Walentowski 2008; Müller and Gossner 2010). Most saproxylic beetle species that prefer moderately to highly decayed wood are assumed to have low host-tree preferences, meaning they inhabit tree hollows in different deciduous tree species (Milberg et al. 2014; Vogel et al. 2021). While tree hollows can occur in most deciduous tree species, they are less common in coniferous trees (Larrieu and Cabanettes 2012) because the strong resin flow of conifers contains compounds that are toxic to potential intruders and usually closes injuries of the bark effectively (Siitonen 2012; Milberg et al. 2014). Hence, for saproxylic beetles living in tree hollows, the landscape surrounding focal tree hollows is composed of patches of potentially suitable habitat (i.e., deciduous forest) and non-habitat (i.e., coniferous forest and open land).

As fragmentation of the landscape has resulted in isolated forest patches that are mostly surrounded by highly contrasting environmental matrices (Shepherd and Brantley 2005; Müller and Gossner 2010), saproxylic beetles must cover the distance between two habitat patches by dispersal. Based on the vulnerability of specialized species to habitat fragmentation (Oleksa et al. 2013; Sverdrup-Thygeson et al. 2017), one would expect the proportion of suitable habitat in the surrounding landscape to be of much larger importance for habitat specialists than generalists. Accordingly, many saproxylic beetle species that are specialized in long-lasting dead wood structures appear to not be able to overcome the distances between forest patches by dispersal (Ranius and Hedin 2001; Jonsson 2012; Oleksa et al. 2015). Jonsson (2000) argues that high and continuous availability of these dead wood structures in ancient times may have led to low selection pressures for efficient dispersal among highly specialized saproxylic beetle species. Therefore, these ancient environmental conditions may have led evolution towards species with narrow habitat demands and low dispersal abilities (Jonsson 2000; Komonen and Müller 2018). Species specialized in long-lasting habitats like tree hollows are assumed to be especially limited in their dispersal ability (the “stability-dispersal hypothesis”; Kirby and Drake 1993; Nilsson and Baranowski 1997; Hedin et al. 2008; Oleksa et al. 2013; Percel et al. 2019). The relationship between degree of specialization and species’ dispersal ability is still subject to discussion (Martin and Fahrig 2018), but several studies on invertebrates have suggested that highly specialized species have lower dispersal abilities than generalist species (Entling et al. 2011; Carnicer et al. 2013; Dapporto and Dennis 2013; Stevens et al. 2014; Dahirel et al. 2015). Thus, many rare saproxylic beetles that specialized in temporally stable but rare habitats like tree hollows might be dispersal-limited, as their ability to establish new populations far from present ones has been shown to be low (Ranius and Hedin 2001; Hedin et al. 2008; Janssen et al. 2016; Percel et al. 2019).

Although we still lack species-specific details on dispersal abilities of most saproxylic beetle species (Feldhaar and Schauer 2018), certain morphological traits of beetles have been assumed to be related to dispersal ability (Gómez-Rodríguez et al. 2015). Body size of beetles has been shown to be a highly integrative trait representing metabolic rate, demographical properties but also dispersal ability as beetle species with a large body size are expected to be better dispersers (Hagge et al. 2019). Additionally, dispersal ability has been assumed to be positively associated with long wings relative to body size, low wing load relative to body size, and high wing aspect ratio (wing length divided by wing width) of beetle species (Hagge et al. 2021; Burner et al. 2023). Human land use can filter species assemblages by selecting against species with particular morphological traits, e.g., through habitat fragmentation and/or ecological degradation of forests (Hagge et al. 2021).

It has been proposed that instead of focusing solely on species richness, the diversity of functional traits of species within a community (functional diversity) should be studied to gain insights on the ecosystem functions and services provides by it (Hooper et al. 2005; Cadotte et al. 2011; Gagic et al. 2015). Furthermore, these functional traits can be response traits that can be analyzed to gain knowledge on potential habitat filters and biotic interactions. A considerable amount of research has been done on predictors of saproxylic beetle species richness in hollow deciduous trees (Ranius 2002; Widerberg et al. 2012; Quinto et al. 2014; Micó et al. 2015; Micó 2018; Schauer et al. 2018b; Henneberg et al. 2021), but predictors of functional diversity have remained largely unexplored (Wetherbee et al. 2020). It is unknown how landscape composition surrounding focal tree hollows affects dispersal-associated morphological traits of the saproxylic beetle communities or their functional diversity, but we expected communities in tree hollows that are located in isolated forest patches or more fragmented forest regions to shift towards species with a better dispersal ability, i.e., beetles with relatively larger body size, longer wings relative to body size, lower wing load, and a higher wing aspect ratio (Hagge et al. 2021; Burner et al. 2023).

In this study we address the following hypotheses: (I) Landscape composition surrounding the focal tree hollows will strongly influence saproxylic beetle species richness in the hollows. We expect tree hollows surrounded by a larger proportion of unsuitable habitats (e.g., open land or forest dominated by conifers) to harbor saproxylic beetle communities with lower diversity. (II) Landscape composition will have a stronger effect on threatened saproxylic beetle species in tree hollows compared to total species richness of saproxylic beetles as threatened species may have a lower dispersal ability. (III) Functional diversity of morphological traits that are associated with dispersal ability will be related to landscape composition surrounding the focal tree hollows. Beetle communities in isolated forest patches or fragmented forest regions are expected to contain a higher proportion of species with a better dispersal ability, reflected by morphological traits associated with dispersal, than communities in less isolated forest stands.

## Materials and methods

### Study sites

The study was conducted in 2018 and 2019 in three Bavarian (Germany) state forest management districts (Bayerische Staatsforsten, BaySF): Ebrach (N 49°50′, E 10°29′), Fichtelberg (N 49°59′, E 11°50′), and Kelheim (N 48°55′, E 11°52′). These state forest management districts were selected because they each display the full range of management intensity from strictly protected forest reserves to intensively managed forests. The three study regions also represent a gradient in tree-species composition from semi-natural mostly deciduous beech and oak forests (Ebrach) to mixed forests (Kelheim) and mostly coniferous forests with a high proportion of planted *Picea abies* trees (Fichtelberg). The latter is typical for central European forests that are managed for wood production (Müller et al. 2008). Thus, the landscape surrounding the focal tree hollows in the three study regions differed significantly regarding the proportion of potentially suitable habitat (i.e., deciduous forest) around the tree hollows (see Fig. 1, Table S5).

The BaySF forest management district Ebrach in the Steigerwald in northern Bavaria consists of temperate deciduous forest stands (app. 1000 km², mean annual temperature: 7–8 °C, mean annual precipitation: 850 mm [Bässler et al. 2014]). The dominant tree species is European beech *Fagus sylvatica* (43% cover), followed by oak (*Quercus robur* and *Q. petraea*, 20%). Deciduous trees cover more than 70% of the forest district area (Müller et al. 2008). The altitude of sampled trees ranged from 324 to 482 m above sea level (a.s.l.).

The BaySF forest management district Fichtelberg is located in the low mountain range Fichtelgebirge and consists of mainly coniferous forest stands (app. 157 km², mean annual temperature: 5–6 °C, mean annual precipitation: 1000–1500 mm [BaySF 2017]), and is characterized by humid, sub-alpine climate. The dominant tree species is Norway spruce *P. abies* (80% cover), followed by European beech (7%) (BaySF 2017). The altitude of sampled trees ranged from 525 to 873 m a.s.l.

The BaySF forest management district Kelheim consists of forest stands that are mixed in tree-species composition with 56% coniferous and 44% deciduous trees (app. 179 km², mean annual temperature: 7–8 °C, mean annual precipitation: 650–850 mm [BaySF 2015]), and is characterized by sub-oceanic climate. Some smaller forest stands in Kelheim are rather isolated, with high proportions of non-forested area (open land, agriculture, towns) surrounding them. The dominant tree species is Norway spruce (44% cover), followed by European beech (29%) (BaySF 2015). The altitude of sampled trees ranged from 396 to 566 m a.s.l.

In each of the three forest management districts, we randomly selected between 41 and 50 European beech trees bearing tree hollows (Ebrach: 50, Fichtelberg: 43, Kelheim: 41) that were distributed over the whole area of each forest management district (see Henneberg

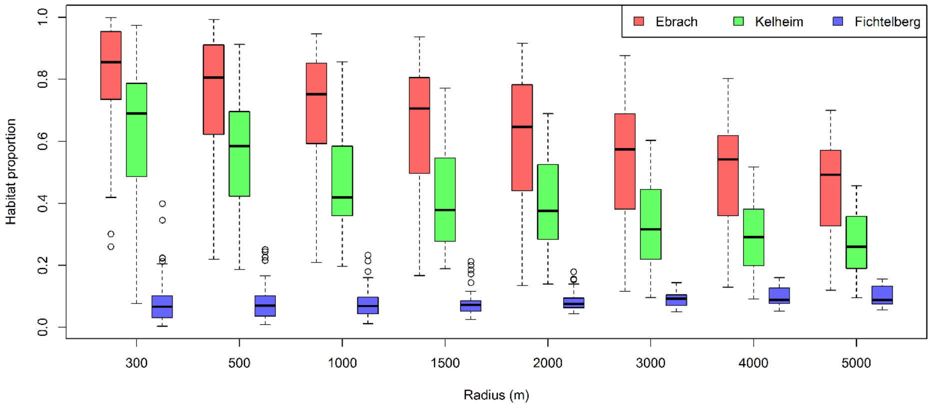


**Fig. 1** Habitat proportion (i.e., proportion of deciduous forest) surrounding the focal tree hollows at radii of 300–5000 m in the three forest regions Ebrach, Fichtelberg, and Kelheim in Bavaria (Germany). Ebrach: $n=50$ tree hollows, Fichtelberg: $n=43$, Kelheim: $n=41$

et al. 2021) (Fig. S1-S3). Tree hollows were selected if they contained at least 2 cm of wood mold at the bottom of each tree hollow, and the diameter at breast height (DBH) of the hollow-bearing tree was larger than 20 cm. Tree hollows included both trunk rot-holes with wood mold and trunk base rot-holes with ground contact (Larrieu et al. 2018). For safety reasons maximum height above the forest floor of the lowest point of the hollow entrance was restricted to 350 cm. The minimum distance between two sampled trees was set to 200 m, and the minimum distance to the forest edge was set to 100 m. Tree hollows matching the criteria were randomly selected in each forest stand by assigning each tree hollow in a given stand a number and rolling a die (see Henneberg et al. 2021).

### Sampling method and identification of saproxylic beetles

After selection of tree hollows in February and March (Ebrach/Fichtelberg: 2018, Kelheim: 2019), all hollows were closed with black acrylic mesh to prevent vertebrates like birds or bats from using them as nesting place. The black acrylic mesh also did not allow insects to pass through. During the sampling period from April to September (18 weeks), all sampled hollows were closed with black cloth and emergence traps (modified from Gouix and Brustel 2012) that allow effective sampling of tree hollow arthropod communities as only individuals emerging from the tree hollows can be trapped (Schauer, Steinbauer et al. 2018). The collecting bottles contained ethanol absolute (>99.8% EtOH) and were emptied biweekly. A beetle taxonomist (Boris Büche) determined all beetles to species-level (see Henneberg et al. 2021).

### Landscape composition assessed via CORINE satellite data

To calculate the proportion of suitable habitat at radii of 300 m to 5000 m around the focal tree hollows we used CORINE satellite data of the three study regions (CORINE high resolution layer: Dominant Leaf Type (DLT), Copernicus Programme, European Environment Agency 2018). The utilized DLT high resolution layer is based on Sentinel-2 A and -B times series (Level-2 A data) satellite data with a spatial resolution of 10 m x 10 m. Using the software ArcGIS Desktop (version 10.8, ESRI 2018) we calculated circular buffers around each tree hollow with the radii 300 m, 500 m, 1000 m, 1500 m, 2000 m, 3000 m, 4000 m, and 5000 m. These spatial scales were not randomly selected or chosen through physical constraints (see Jackson & Fahrig 2015) but were based on biological reasons (Holland et al. 2005). Dispersal distances of saproxylic beetles, although known for only a few species, are assumed to range from a few meters to a few kilometers (Feldhaar and Schauer 2018), and we chose the range of spatial scales accordingly. As most saproxylic beetles are not assumed to be host-specific regarding tree species but rather specialized in dead wood of either deciduous or coniferous trees (Milberg et al. 2014; Vogel et al. 2021), proportion of deciduous forest in the surrounding landscape can be used as a proxy for suitable habitat for hollow-dwelling beetle species. Furthermore, tree hollows are far more common in deciduous than in coniferous trees (Larrieu and Cabanettes 2012; Siitonen 2012). Therefore, we classified deciduous forests as potential "habitat" and the proportion of coniferous forest and open land as "non-habitat". We calculated the proportion of deciduous forest (=habitat proportion) for each circular buffer around the focal tree hollows as well as the overall proportion of forest. Habitat proportion around the tree hollows was then used as explanatory variable in generalized linear models (GLM) with species richness or morphological trait indices of saproxylic beetles in tree hollows as dependent variable. We also included the overall forest proportion as covariable in the models to better isolate the effect of potential habitat.

We are aware that focusing solely on surrounding habitat and forest proportion at different spatial scales to explain saproxylic beetle species richness in tree hollows would represent a strong simplification of the ecological interactions in managed forests. Furthermore, it is difficult to isolate the effects of the surrounding landscape from effects of local tree hollow quality. Therefore, we included two statistically significant covariates from our previous study (see Henneberg et al. 2021) that represent local habitat quality, namely "size of tree hollow entrance" and "height of hollow entrance above the ground", to improve model performance and better define the relationship of hollow-dwelling saproxylic beetles with surrounding habitat proportion. Some studies have suggested that there are no interactive effects of local habitat quality with landscape habitat proportion, but that each additively influence saproxylic beetle species richness (Seibold et al. 2017; Cours et al. 2022; Traylor et al. 2023).

## Morphological traits and functional diversity of saproxylic beetles

Morphological traits of beetle species that were sampled in the tree hollows were analyzed using the comprehensive trait database generated by Hagge et al. (2021). In this database, 32 morphological traits of 1,170 saproxylic beetle species mostly collected in Europe were measured directly and five additional traits (wing load, wing aspect, mandibular aspect ratio, total hairiness, and body roundness) were calculated based on the measured values (a detailed measurement protocol and the morphological trait database of saproxylic beetles are published on Dryad Digital Repository https://doi.org/10.5061/dryad.2fqz612p3; Hagge et al. 2021).

To analyze the effects of landscape composition on single morphological traits that are associated with better dispersal ability (large body size, long wings relative to body size, low wing load relative to body size, high wing aspect ratio) (Hagge et al. 2021), we calculated community-weighted means (CWM) for each of the four traits and for each tree hollow using the function *weighted_mean* in the *stats* package.

Based on the same four morphological traits, we calculated three functional diversity indices that measure different aspects of functional diversity, using the dbFD function in the R package FD (Laliberté and Shipley 2014): (1) Functional dispersion (FDis) represents the mean distance in multidimensional trait space of individual species to the centroid of all species; it can account for species' abundances by shifting the position of the centroid toward the more abundant species and weighting distances of individual species by their relative abundances (Laliberté and Legendre 2010). FDis is the multivariate analogue of the weighted mean absolute deviation (MAD); this makes the index unaffected by species richness by construction (Laliberté and Legendre 2010). (2) Functional evenness (FEve) measures the regularity of distribution and relative abundance of species in the functional trait space (Villéger et al. 2008). (3) Functional richness (FRic) represents the range of traits in a community quantified by the volume of functional trait space occupied (Villéger et al. 2008).

## Statistical analysis

All analyses were performed with the software R, version 4.4.1 (R Core Team 2024). To test for spatial independency of the data, spatial autocorrelation of the explanatory variables was analyzed in each of the three forest regions using the function *Moran.I* in the package *APE* (Paradis et al. 2004). Since spatial autocorrelation of the explanatory variables was detected, we included a second-order trend surface to the models by adding the geographic coordinates and their interaction to account for spatial autocorrelation (Hothorn et al. 2011). To test for differences in habitat proportion surrounding the focal tree hollows in the three study regions, an ANOVA was implemented and followed by a post-hoc pairwise t-test. Generalized linear models (GLM) with Poisson (log-link) error distribution were implemented to analyze the influence of surrounding habitat proportion on total species richness of saproxylic beetles in the tree hollows and on species richness of the subset of threatened saproxylic beetles, i.e., species of category G (threatened to an unknown extent) and higher (G, VU, EN, CR) in the Red List of Germany (Ries et al. 2021) or the Red List of Bavaria (2006). Two parameters of local tree hollow quality that have been shown to have a significant influence on species richness in the hollows in a previous study, namely “size of tree hollow entrance” and “height of the hollow entrance above ground” (see Henneberg et al. 2021), were included as explanatory variables in the models to be able to isolate the effect of the surrounding landscape from local habitat quality. GLMs with Gamma (log-link) error distribution were implemented to test the influence of surrounding habitat proportion and local habitat quality (“size of the entrance”, “height above ground”) on community-weighted means (CWM) of saproxylic beetles’ dispersal-associated morphological traits (body size, relative wing length, relative wing load, wing aspect) and functional diversity indices (FDiv, FEve, and FRic). For each study region and each response variable, an independent GLM was fitted for each radius of surrounding habitat proportion (300 m, 500 m, 1000 m, 1500 m, 2000 m, 3000 m, 4000 m, 5000 m). Models with a Poisson error distribution were tested for overdispersion using the function *dispersion.test* in the package *AER* (Kleiber and Zeileis 2008). If overdispersion was detected, a negative binomial distribution was applied using the function *glm.nb* in the package *MASS* (Ripley et al. 2013). To clarify the statistically significant results of models with FRic as dependent variable in Fichtelberg and Kelheim, CWM of body size and relative wing length of beetle communities of the 15 tree hollows with the lowest proportion of habitat in their surroundings was compared to those of the 15 hollows surrounded by the largest proportions of habitat in each of the two forest regions using t-test. Distribution of all model residuals was inspected visually. Explanatory variables of surrounding habitat proportion that showed a significant relationship with the dependent variable in the GLMs were visualized using the package *visreg* (Breheny and Burchett 2017). All analyses were performed for total species richness of saproxylic beetles as well as species richness of the subset of threatened species according to the Red List of Germany (Ries et al. 2021) or the Red List of Bavaria (2006). To visualize and compare the saproxylic beetle species richness and species composition in the three forest regions, a Venn diagram was generated showing total species richness of saproxylic beetles and species richness of threatened saproxylic beetles using the package *VennDiagram* (Chen and Boutros 2011).

## Results

### Landscape composition (300–5000 m radius)

The proportion of deciduous forest and therefore the proportion of suitable habitat at radii of 300 m to 5000 m around each tree hollow differed strongly between the three forest regions: ANOVA $p<0.001$ (df=2, F=52.61) (pairwise t-test: Ebrach - Kelheim: $p<0.01$, Ebrach - Fichtelberg: $p<0.001$, Kelheim - Fichtelberg: $p<0.001$) (Table S5). In Ebrach the proportion of deciduous forest around the focal tree hollows was much higher across all radii compared to the other two forest regions. In Fichtelberg, where the tree-species composition is dominated by coniferous tree species, surrounding habitat proportion was close to zero across all radii around the tree hollows (Fig. 1).

### Saproxylic beetle species composition

A total of 254 species (5880 individuals) of saproxylic beetles were collected from the 134 tree hollows (Ebrach: 196 species, $n=50$ tree hollows; Fichtelberg: 74 species, $n=43$; Kelheim: 107 species, $n=41$) (Table S4). 52 species (20.5%) were regarded as threatened (Ebrach: 41 species (20.9%), Kelheim: 27 species (25.2%), Fichtelberg: 9 species (12.2%) (Ries et al. 2021). Species richness and species composition differed substantially between the three forest regions (Fig. 2).

### Ebrach forest management district

In Ebrach there was no relationship between total species richness of saproxylic beetles in the tree hollows and the proportion of suitable habitat surrounding the hollows at any spatial scale from 300 m to 5000 m (Table S1).

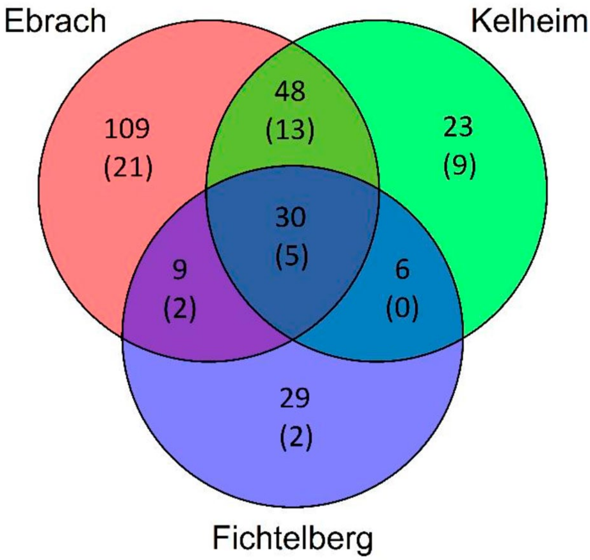


**Fig. 2** Venn diagram comparing the saproxylic beetle species richness (threatened species richness) and species composition in the three forest regions in Bavaria, Germany. Ebrach: 196 species (41 threatened species) ($n=50$ tree hollows), Fichtelberg: 74 species (9 threatened species) ($n=43$), Kelheim: 107 species (27 threatened species) ($n=41$)

When only the 41 threatened saproxylic beetle species were included in the models, the relationship with habitat proportion surrounding the focal tree hollows was much more pronounced. There was a significant positive relationship between surrounding habitat proportion and species richness of threatened saproxylic beetles for all radii ranging from 300 m to 5000 m around the focal tree hollows (Fig. 3, Table S1). The pseudo-R² values, showing the explanatory power of the models, ranged from 0.114 (*r*=500 m) to 0.194 (*r*=5000 m) (Fig. 3, Table S1).

## Fichtelberg forest management district

In Fichtelberg there was no relationship between total species richness of saproxylic beetles in the tree hollows and the proportion of suitable habitat surrounding the hollows at any spatial scale from 300 m to 5000 m (Table S1).

When only the nine threatened saproxylic beetle species were included in the analysis, similar to Ebrach, the relationship with surrounding habitat proportion was much more pronounced. There was a significant positive relationship between surrounding habitat proportion and species richness of threatened saproxylic beetles for all radii ranging from 300 m to 4000 m around the focal tree hollows (Fig. 4, Table S1). The pseudo-R² values, showing the explanatory power of the models, ranged from 0.189 (*r*=4000 m) to 0.393 (*r*=500 m) (Fig. 4, Table S1).

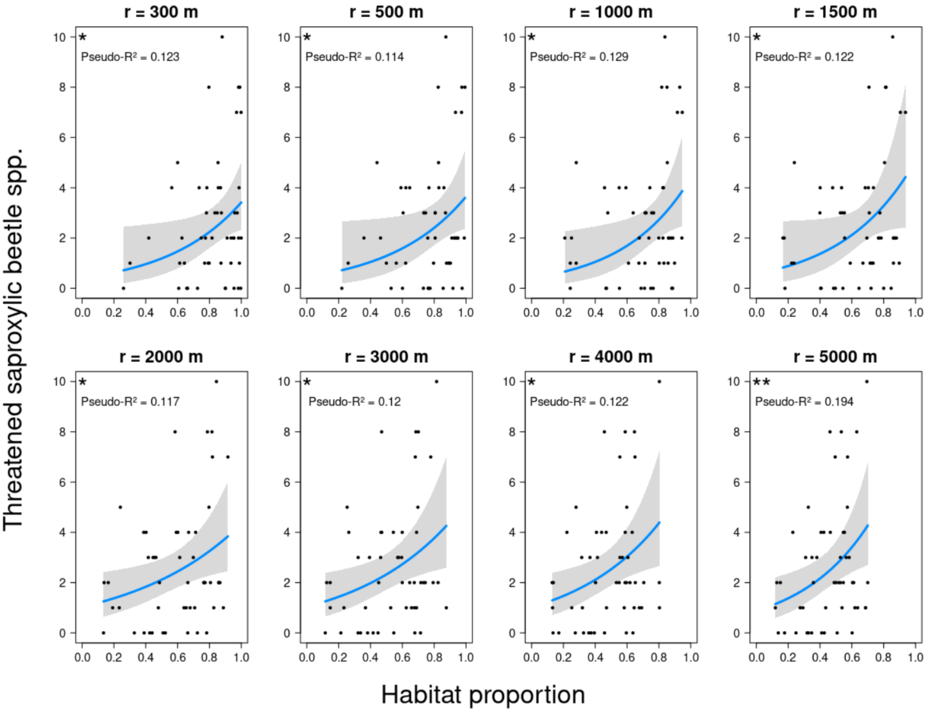


**Fig. 3** GLMs of the Ebrach forest management district. Species richness of threatened saproxylic beetles as dependent variable; habitat proportion at different radii around the focal tree hollows (*n*=50) as explanatory variable. $p<0.05$ (*), $p<0.01$ (**). Pseudo-² values show the explanatory power of each model

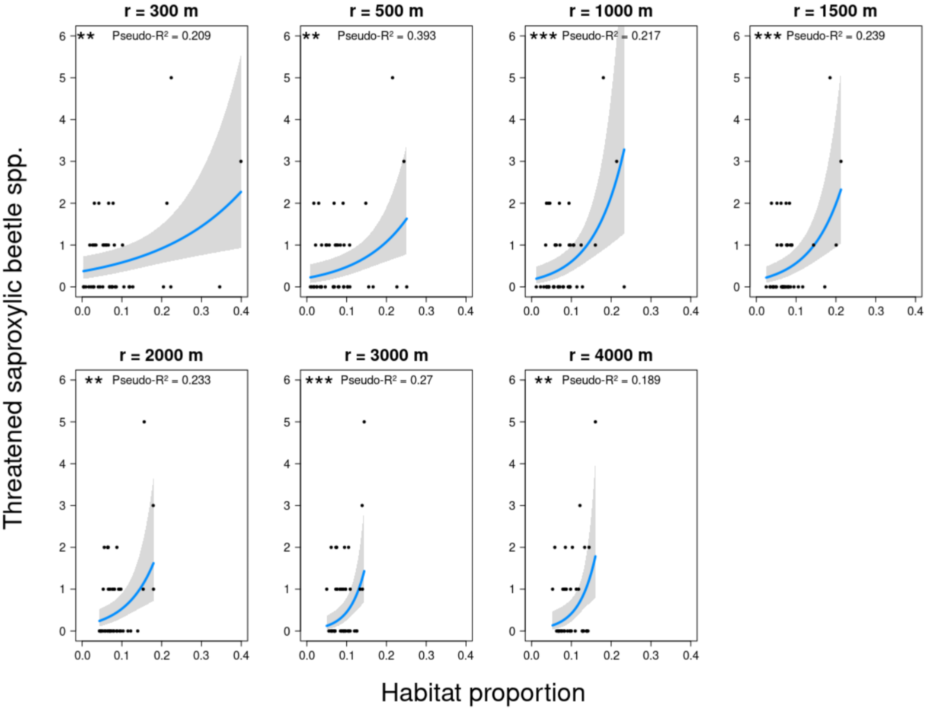


**Fig. 4** GLMs of the Fichtelberg forest management district. Species richness of threatened saproxylic beetles as dependent variable; habitat proportion at different radii around the focal tree hollows ($n=43$) as explanatory variable. $P<0.01$ (**), $p<0.001$ (***). Pseudo-$R^2$ values show the explanatory power of each model

## Kelheim forest management district

In Kelheim there was no relationship between total species richness of saproxylic beetles in the tree hollows and the proportion of suitable habitat surrounding the hollows at any spatial scale from 300 m to 5000 m. There were also no significant relationships between surrounding habitat proportion and species richness when only the 27 threatened saproxylic beetle species were included in the analysis (Table S1).

## Effects of the proportion of suitable habitat around the tree hollows on morphological traits and functional diversity of saproxylic beetle communities in the hollows

There were no statistically significant relationships between surrounding habitat proportion and the community weighted mean (CWM) of any single dispersal-associated morphological trait.

Regarding functional diversity, we detected statistically significant relationships between the beetles' functional richness (FRic) and the proportion of suitable habitat at different radii around the focal tree hollows in the forest regions Fichtelberg and Kelheim. In the Fichtelberg forest region, the proportion of suitable habitat surrounding the tree hollows

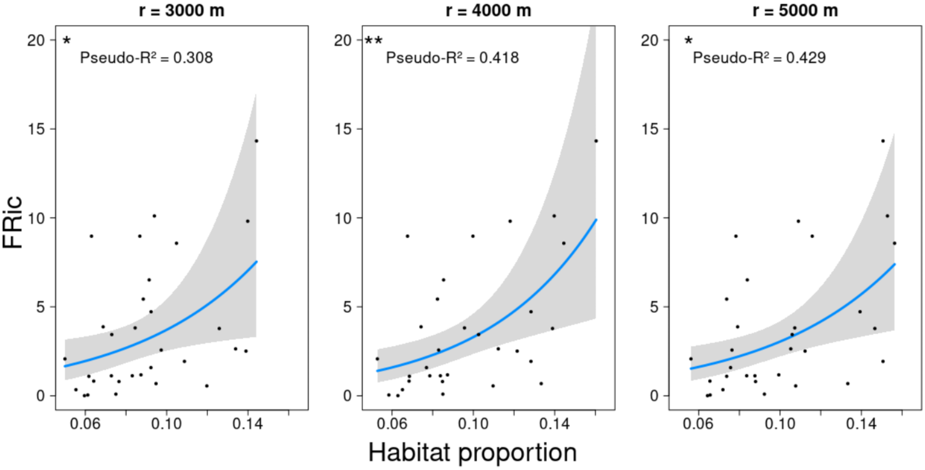
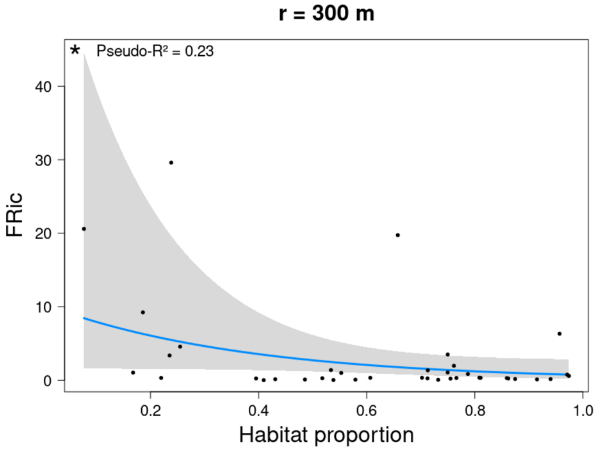


**Fig. 5** GLMs of the Fichtelberg forest management district. Functional richness (FRic) of saproxylic beetles as dependent variable; habitat proportion at radii of 3000 m, 4000 m, and 5000 m around the focal tree hollows ($n=43$) as explanatory variable. $p<0.05$ (*), $p<0.01$ (**). Pseudo-R² values show the explanatory power of the models

**Fig. 6** GLM of the Kelheim forest management district. Functional richness (FRic) of saproxylic beetles as dependent variable; habitat proportion at a radius of 300 m around the focal tree hollows ($n=41$) as explanatory variable. $p<0.05$ (*). The pseudo-R² value shows the explanatory power of the model



at large spatial scales of 3000 m ($p<0.05$), 4000 m ($p<0.01$), and 5000 m ($p<0.05$) radius showed a positive relationship with the beetles' functional richness (Fig. 5, Table S2). Pseudo- R² values showing the explanatory power of the models were 0.308 ($r=3000$ m), 0.418 ($r=4000$ m), and 0.429 ($r=5000$ m) (Fig. 5, Table S2). In the Kelheim forest region, the proportion of suitable habitat surrounding the tree hollows at the smallest spatial scale of 300 m ($p<0.05$) showed a negative relationship with the beetles' functional richness (Fig. 6, Table S2). The pseudo-R² value showing the explanatory power of the model was 0.231 (Fig. 6, Table S2). There were no effects of surrounding habitat proportion on the other two multi-trait-based functional diversity indices (functional dispersion, FDis; functional evenness, FEve) (Table S2).

The t-test comparison of the CWM of body size and relative wing length of the 15 tree hollows with the lowest proportion of habitat in their surroundings to those of the 15 hollows surrounded by the largest proportion of habitat showed no statistically significant differences. However, in Fichtelberg there was a trend towards larger body size ($p=0.07$) and larger relative wing length ($p=0.092$) when there were low proportions of habitat in the surroundings. In Kelheim no trend could be detected.

## Discussion

To better understand how to conserve saproxylic beetle assemblages in tree hollows in central European managed forests, we have tested the effect of the proportion of potentially suitable habitat, i.e., deciduous forest, at spatial scales of 300–5000 m around the focal tree hollows, on species richness and dispersal-associated morphological traits of saproxylic beetles in the hollows. We found positive relationships between species richness of threatened species and surrounding habitat proportion in two of the three study regions, indicating an increased sensitivity of threatened hollow-dwelling saproxylic beetles to surrounding landscape composition. The highest explanatory power of surrounding habitat proportion for species richness of threatened hollow-dwelling species was obtained in the Fichtelberg study region characterized by the lowest proportions of suitable habitat of the three study regions. Furthermore, we detected relationships between the beetles' dispersal-associated functional richness (FRic) and surrounding habitat proportion in two of the three study regions. In the Fichtelberg study region, a connected forest region consisting of mostly coniferous trees, FRic increased with surrounding habitat proportion, indicating better dispersal ability of hollow-dwelling saproxylic beetle species when there are low proportions of potentially suitable habitat available in the surrounding landscape. In the Kelheim forest region, characterized by small and isolated patches of forest, FRic increased with decreasing surrounding habitat proportion, indicating no increasing dispersal ability of hollow-dwelling beetle communities when habitat patches are surrounded by open land.

### Effects of surrounding landscape composition on species richness in the tree hollows

We detected a positive relationship between surrounding habitat proportion and saproxylic beetle species richness in the tree hollows, specifically regarding the richness of threatened species in the Ebrach and Fichtelberg study regions. Threatened saproxylic beetle species richness was positively affected by surrounding habitat proportion at spatial scales from 300 m to 5000 m around the focal tree hollows in the Ebrach study region that is characterized by the highest proportion of deciduous forest (i.e., potential habitat) surrounding the tree hollows, and from 300 m to 4000 m around the focal tree hollows in the Fichtelberg region that is characterized by the lowest proportion of deciduous forest surrounding the tree hollows. These findings are in line with results of previous studies that reported positive relationships between the availability of dead wood habitats at a landscape scale and saproxylic beetle species richness (Sverdrup-Thygeson et al. 2014), especially for threatened species (Götmark et al. 2011; Ranius et al. 2011). Total species richness of saproxylic beetles was not affected by surrounding habitat proportion in any of the three study regions.

The relationships between surrounding habitat proportion and species richness of threatened saproxylic beetles in the Fichtelberg study region could be due to low proportions of deciduous forest in that particular study region where few deciduous trees are scattered in a matrix of coniferous forest. With such low proportions of potentially suitable habitat available in the surrounding landscape, even small numbers of deciduous trees in the surrounding of the focal tree hollows seem to matter as potential habitat for threatened saproxylic beetle species. In general, the Fichtelberg study region showed the lowest species richness of saproxylic beetles out of the three forest regions in our study which could be additionally due to its sub-alpine climate. The results exemplify that conservation efforts should also focus on increasing the proportions of deciduous trees in managed forests as tree hollows will have a lower probability to be colonized by saproxylic beetle species if they are isolated within a matrix of coniferous trees. In a context of overall low habitat amount, any additional amount of habitat would matter for species richness of saproxylic beetles. In forest regions comprising mostly of coniferous trees, like the Fichtelberg study region, saproxylic biodiversity might also benefit from an implementation of Triad landscape zoning as suggested by Blattert et al. (2023). The authors state that saproxylic biodiversity might benefit from a zoning of 20% intensively managed forest, 50% extensively used forest and 30% strict forest reserves at the landscape level. This “land-sparing and land sharing” concept could have strong positive effects on saproxylic biodiversity by adding suitable habitats within intensively managed areas (Blattert et al. 2023). Extending the areas of strict forest reserves where trees can grow older beyond the short rotation times of managed forests would probably benefit hollow-dwelling saproxylic beetles as old forests have been shown to be disproportionally important for saproxylic beetle biodiversity (Traylor et al. 2023).

Highly specialized species of saproxylic beetles, like tree hollow specialists that obligatorily depend on tree hollows, include a higher proportion of threatened species than generalist species (Schmidl and Büche 2018). Additionally, highly specialized saproxylic beetle species rely more on certain habitat conditions and resources than generalist species (Müller et al. 2005; Gossner and Müller 2011) and show a higher vulnerability to habitat fragmentation (Sverdrup-Thygeson et al. 2017). Furthermore, it has been assumed that saproxylic beetle species that are specialized in long-living habitats like tree hollows have evolved rather low dispersal abilities (the “stability-dispersal hypothesis”) (Ranius and Hedin 2001; Hedin et al. 2008; Jonsson 2012; Stevens et al. 2014; Oleksa et al. 2015; Percel et al. 2019). Therefore, we expected threatened species to depend more on habitat availability within the surrounding landscape (Götmark et al. 2011; Jacobsen et al. 2015) and react more sensitively to surrounding habitat proportion compared to generalist species (Sverdrup-Thygeson et al. 2017). This expectation was confirmed in our study, underpinning that threatened saproxylic beetle species need more conservation efforts at large spatial scales than common species (Ranius et al. 2011).

In the Kelheim study region that is characterized by mixed forest stands containing deciduous and coniferous tree species at an almost equal proportion, neither total species richness nor threatened species richness was affected by surrounding habitat proportion. This result could be accredited to the high heterogeneity in composition of forest stands in that particular study region where patches of deciduous forest might be too fragmented and small for vital populations of hollow-dwelling saproxylic beetles to persist (extinction threshold hypothesis; Fahrig 2002).

Our study shows that while all species of saproxylic beetles have to cope with the loss of diverse dead wood habitats in central European forests, especially the threatened saproxylic beetle species living in tree hollows react sensitively to surrounding landscape composition, making this group more vulnerable to habitat fragmentation, habitat degradation, and habitat loss.

### Effects of landscape composition on dispersal-associated morphological traits and functional diversity of beetles

Human land use can filter saproxylic beetle species assemblages by selecting against species with particular morphological traits, e.g., through habitat fragmentation or ecological degradation of forests (Hagge et al. 2021). We tested this assumption in our study system of three forest regions. Our hypothesis was that tree hollows that are located in small and isolated forest patches in fragmented forest regions (e.g., the Kelheim forest region), or those isolated within a matrix of coniferous forest (e.g., in the Fichtelberg forest region), would contain saproxylic beetle communities that shift towards species with a better dispersal ability and morphological traits facilitating dispersal, compared to communities in large and connected deciduous forest stands. This hypothesis was only partially confirmed in our study. Few relationships between landscape composition and functional diversity were detected in the forest region Fichtelberg, where small patches of deciduous forest were surrounded by coniferous forest, and the fragmented Kelheim forest region, where forest patches were surrounded by open land, agriculture, or towns. Results of other studies have also shown mixed support for the expected effects of surrounding landscape parameters on saproxylic beetles' dispersal-associated morphological traits like body size and wing morphology (Gibb et al. 2006; Bouget et al. 2015; Cours et al. 2022; Burner et al. 2023; Wetherbee et al. 2020). One possible explanation could be that functional diversity metrics (except for FRic) are often driven by the most common or abundant species and often do not reflect community-wide trait-niche relationships (Burner et al. 2023). Another possible explanation is that there is a large amount of unexplained phylogenetic signal, which indicates that important traits (behavioral, physiological, or morphological) are not being accounted for and these may be more important than, e.g., wing morphology (Burner et al. 2023).

In the mostly coniferous Fichtelberg forest region, functional richness (FRic) was positively related to the proportion of suitable habitat surrounding the focal tree hollows at large radii of 3000 m, 4000 m, and 5000 m. Thus, when there were only small proportions of deciduous forest embedded in a matrix of coniferous forest in the surrounding of a focal tree hollow, the dispersal-associated FRic of beetle communities decreased. Hence, beetle communities in tree hollows were more similar regarding their dispersal-associated traits when availability of suitable habitat in the surroundings was very limited. However, "more similar regarding their dispersal-associated traits" could suggest both better or worse dispersal abilities. Therefore, we compared the CWM of body size and relative wing length of the 15 tree hollows with the lowest proportion of habitat in their surroundings to that of the 15 hollows surrounded by the largest proportions of habitat. Although the results were not significant, the trend showed that with less suitable habitat (i.e., more coniferous forest) surrounding a focal tree hollow, the CWM of the dispersal-associated traits body size and relative wing length of saproxylic beetle communities inhabiting the hollow were suggestive of a possible increase. This trend supports our hypothesis that tree hollows that are isolated within a matrix of coniferous forest might contain saproxylic beetle communities that shift towards species with a better dispersal ability.

In contrast, in the fragmented Kelheim forest region characterized by mixed deciduous and coniferous forest stands surrounded by open land, FRic was negatively related to surrounding habitat proportion at the smallest radius of 300 m around the focal tree hollows. Thus, FRic in the tree hollows increased when proportions of suitable habitat surrounding the focal tree hollows at small radii in this fragmented forest region decreased. Hence, beetle communities were less similar regarding their dispersal-associated traits when availability of suitable habitat in the near surrounding of a focal tree hollow was low. Since the Kelheim forest region was fragmented and small forest patches were surrounded by open land, this finding might indicate that some hollow-dwelling saproxylic beetle species do not readily disperse across open land. The fact that this relationship was statistically significant only at the smallest spatial scale of 300 m around the focal tree hollows might reflect the small size of many forest patches in the fragmented Kelheim study region, as opposed to the large, connected forest area in the Fichtelberg region. The comparison of CWM of body size and relative wing length of the 15 tree hollows with the lowest proportion of suitable habitat to that of the 15 hollows with largest proportions of surrounding habitat supported our assumption: there was no difference in body size and relative wing length between the hollows with low proportions of suitable habitat in their surroundings (i.e., more open land) and those with larger proportions of forest surrounding them. This might imply that tree hollows that are isolated and surrounded by open land do not contain saproxylic beetle communities that shift towards species with a good dispersal ability as some species might not disperse across open land. Therefore, beetle communities in isolated forest patches might benefit from increased connectivity among suitable habitat patches as shown by Oleksa et al. (2015) for saproxylic beetle communities in tree hollows in rural avenues. In the mostly coniferous Fichtelberg forest region, although tree hollows were also surrounded by unsuitable habitat, there was still forest (coniferous forest) surrounding the focal tree hollows which might not hinder saproxylic beetle species with good dispersal abilities from reaching distant patches of deciduous trees.

## Conclusions

Implications for forest management and conservation practice that can be derived from this study include the awareness that a higher proportion of potential habitat (in this study: deciduous forest) will be especially beneficial for highly specialized and threatened saproxylic beetle species. Therefore, an increase in the proportion of deciduous forest as well as an increase in dead wood amount in central European forests will support threatened species of saproxylic beetles that are most vulnerable and in need of effective conservation measures.

Moreover, as threatened saproxylic beetle species reacted more sensitively to large-scale landscape composition than common species, efforts to protect threatened saproxylic beetle species should not only include single forest stands but focus on the landscape scale, especially in the light of ongoing habitat fragmentation and forest degradation in central Europe.

Finally, results from more isolated habitat patches in the Fichtelberg and Kelheim forest regions imply that some saproxylic beetle species might not readily disperse across open land. Therefore, a general increase in forest connectivity by increasing linear woody structures or forest cover – be it deciduous or coniferous forest – would greatly support the dispersal of hollow-dwelling saproxylic beetle species.

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**Data availability** The data that support the findings of this study are openly available in figshare at https://figshare.com/s/b57a9b4cd8bf8118ebd1.

## Declarations

**Competing interests** The authors declare no competing interests.

## References

Bässler C, Ernst R, Cadotte M, Heibl C, Müller J (2014) Near-to-nature logging influences fungal community assembly processes in a temperate forest. J Appl Ecol 51:939–948

BaySF (2017) Naturschutzkonzept für den Forstbetrieb Fichtelberg, Stand Februar 2017. Bayerische Staatsforsten. Last visited: 10/13/2023. https://www.baysf.de/fileadmin/user_upload/01-ueber_uns/05-standorte/FB_Fichtelberg/Naturschutzkonzept_Forstbetrieb_Fichtelberg.pdf

BaySF (2015) Regionales Naturschutzkonzept für den Forstbetrieb Kelheim, Stand Mai 2015. Bayerische Staatsforsten. Last visited: 10/13/2023. https://www.baysf.de/fileadmin/user_upload/01-ueber_uns/05-standorte/FB_Kelheim/15_05_20_Endfassung_NSK_FB_Kelheim_.pdf

Blattert C, Eyvindson K, Mönkkönen M, Raatikainen KJ, Triviño M, Duflot R (2023) Enhancing multifunctionality in European boreal forests: the potential role of triad landscape functional zoning. J Environ Manage 348:119250

Bouget C, Brin A, Tellez D, Archaux F (2015) Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. Oecologia 177:911–920

Breheny P, Burchett W (2017) Visualization of regression models using Visreg. R J 9:56

Brunet J, Isacsson G (2009) Restoration of Beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution. Biodivers Conserv 18:2387–2404

Burner RC, Stephan JG, Drag L, Potterf M, Birkemoe T, Siitonen J, Müller J, Ovaskainen O, Sverdrup-Thygeson A, Snäll T (2023) Alternative measures of trait–niche relationships: A test on dispersal traits in saproxylic beetles. Ecol Evol 13:e10588

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087

Carnicer J, Stefanescu C, Vila R, Dincă V, Font X, Peñuelas J (2013) A unified framework for diversity gradients: the adaptive trait continuum. Glob Ecol Biogeogr 22:6–18

Chen H, Boutros PC (2011) VennDiagram: a package for the generation of highly customizable Venn and Euler diagrams in R. BMC Bioinformatics 12:1–7

Cours J, Sire L, Ladet S, Martin H, Parmain G, Larrieu L, Moliard C, Lopez-Vaamonde C, Bouget C (2022) Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales. Landscape Ecol 37:2025–2043

Dahirel M, Olivier E, Guiller A, Martin MC, Madec L, Ansart A (2015) Movement propensity and ability correlate with ecological specialization in European land snails: comparative analysis of a dispersal syndrome. J Anim Ecol 84:228–238

Dapporto L, Dennis RL (2013) The generalist–specialist continuum: testing predictions for distribution and trends in British butterflies. Biol Conserv 157:229–236

Entling MH, Stämpfli K, Ovaskainen O (2011) Increased propensity for aerial dispersal in disturbed habitats due to intraspecific variation and species turnover. Oikos 120:1099–1109

ESRI (2018) ArcGIS desktop: version 10.6. Environmental Systems Research Institute

European Environment Agency (2018) Copernicus programme: CORINE HR Dominant Leaf Type 2018, Copenhagen, Denmark. URL: https://land.copernicus.eu/pan-european/high-resolution-layers/forests/dominant-leaf-type

Fahrig L (2002) Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecol Appl 12:346–353

Feldhaar H, Schauer B (2018) Dispersal of saproxylic insects. In: Ulyshen MD (ed) Saproxylic insects: diversity, ecology and conservation. Springer, Cham, pp 515–546

Franc N, Götmark F, Økland B, Nordén B, Paltto H (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biol Conserv 135:86–98

Gagic V, Bartomeus I, Jonsson T, Taylor A, Winqvist C, Fischer C, Slade EM, Steffan-Dewenter I, Emmerson M, Potts SG, Tscharntke T, Weisser W, Bommarco R (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142620

Gibb H, Hjältén J, Ball JP, Pettersson RB, Landin J, Alvini O, Danell K (2006) Wing loading and habitat selection in forest beetles: are red-listed species poorer dispersers or more habitat-specific than common congenerics? Biol Conserv 132:250–260

Gómez-Rodríguez C, Freijeiro A, Baselga A (2015) Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. J Biogeogr 42:1526–1537

Gonthier DJ, Ennis KK, Farinas S, Hsieh HY, Iverson AL, Batáry P, Rudolphi J, Tscharntke T, Cardinale BJ, Perfecto I (2014) Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the Royal Society B: Biological Sciences* 281: 20141358

Gossner MM, Müller J (2011) The influence of species traits and q-metrics on scale-specific β-diversity components of arthropod communities of temperate forests. Landscape Ecol 26:411–424

Gossner MM, Lachat T, Brunet J, Isacsson G, Bouget C, Brustel H, Brandl R, Weisser WW, Müller J (2013) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in Beech forests. Conserv Biol 27:605–614

Götmark F, Åsegård E, Franc N (2011) How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. For Ecol Manag 262:2297–2305

Gouix N, Brustel H (2012) Emergence trap, a new method to survey *Limoniscus Violaceus* (Coleoptera: Elateridae) from Hollow trees. Biodivers Conserv 21:421–436

Hagge J, Abrego N, Bässler C, Bouget C, Brin A, Brustel H, Christensen M, Gossner M, Heilmann-Clausen J, Horák J, Gruppe A, Isacsson G, Köhler F, Lachat T, Larrieu L, Schlaghamersky J, Thorn S, Zapponi L, Müller J (2019) Congruent patterns of functional diversity in saproxylic beetles and fungi across European Beech forests. J Biogeogr 46:1054–1065

Hagge J, Müller J, Birkemoe T, Buse J, Gossner M, Gruppe A, Heibl C, Jarzabek-Müller A, Seibold S, Siitonen J, Soutinho J, Sverdrup-Thygeson A, Thorn S, Drag L (2021) What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. J Anim Ecol 90:1934–1947

Hedin J, Ranius T, Nilsson SG, Smith HG (2008) Restricted dispersal in a flying beetle assessed by telemetry. Biodivers Conserv 17:675–684

Henneberg B, Bauer S, Birkenbach M, Mertl V, Steinbauer MJ, Feldhaar H, Obermaier E (2021) Influence of tree Hollow characteristics and forest structure on saproxylic beetle diversity in tree Hollows in managed forests in a regional comparison. Ecol Evol 11:17973–17999

Holland JD, Fahrig L, Cappuccino N (2005) Body size affects the Spatial scale of habitat–beetle interactions. Oikos 110:101–108

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hothorn T, Müller J, Schröder B, Kneib T, Brandl R (2011) Decomposing environmental, Spatial, and Spatiotemporal components of species distributions. Ecol Monogr 81:329–347

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeograph 24(1):52–63

Jacobsen RM, Sverdrup-Thygeson A, Birkemoe T (2015) Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. J Insect Conserv 19:1053–1062

Janssen P, Cateau E, Fuhr M, Nusillard B, Brustel H, Bouget C (2016) Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. Biodivers Conserv 25:1167–1185

Jonsson BG (2000) Availability of coarse Woody debris in a boreal old-growth *Picea abies* forest. J Veg Sci 11:51–56

Jonsson BG (2012) Population dynamics and evolutionary strategies. In: Stokland JN, Siitonen J, Jonsson BG (eds) Biodiversity in dead wood. Cambridge University Press, Cambridge, pp 338–355

Kirby KJ, Drake CM (1993) Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. English Nature, Peterborough, United Kingdom, p 105

Kleiber C, Zeileis A (2008) Applied econometrics with R. Springer Science & Business Media, New York

Koch Widerberg MK, Ranius T, Drobyshev I, Nilsson U, Lindbladh M (2012) Increased openness around retained Oaks increases species richness of saproxylic beetles. Biodivers Conserv 21:3035–3059

Komonen A, Müller J (2018) Dispersal ecology of Deadwood organisms and connectivity conservation. Conserv Biol 32:535–545

Lachat T, Müller J (2018) Importance of primary forests for the conservation of saproxylic insects. In: Ulyshen MD (ed) Saproxylic insects: diversity, ecology and conservation. Springer, Cham, pp 581–605

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Shipley B (2014) R-package FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Foundation for Statistical Computing, Vienna, Austria

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Can J for Res 42:1433–1445

Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, Krumm F, Lachat T, Michel AK, Regnery B, Vandekerkhove K (2018) Tree related microhabitats in temperate and mediterranean European forests: A hierarchical typology for inventory standardization. Ecol Ind 84:194–207

Lindenmayer DB, Laurance WF, Franklin JF (2012) Global decline in large old trees. Science 338:1305–1306

Martin AE, Fahrig L (2018) Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. Ecology 99:2058–2066

Micó E (2018) Saproxylic insects in tree hollows. In: Ulyshen MD (ed) Saproxylic insects: diversity, ecology and conservation. Springer, pp 693–727

Micó E, García-López A, Brustel H, Padilla A, Galante E (2013) Explaining the saproxylic beetle diversity of a protected mediterranean area. Biodivers Conserv 22:889–904

Micó E, García-López A, Sánchez A, Juárez M, Galante E (2015) What can physical, biotic and chemical features of a tree Hollow tell Us about their associated diversity? J Insect Conserv 19:141–153

Milberg P, Bergman KO, Johansson H, Jansson N (2014) Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. Insect Conserv Divers 7:508–522

Müller J, Gossner MM (2010) Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. Biol Conserv 143:625–633

Müller J, Bußler H, Bense U, Brustel H, Flechtner G, Fowles A, Kahlen M, Möller G, Mühle H, Schmidl J, Zabransky P (2005) Urwald relict species—saproxylic beetles indicating structural qualities and habitat tradition. Waldoekologie Online 2:106–113

Müller J, Bußler H, Kneib T (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a Beech forest in Southern Germany. J Insect Conserv 12:107

Müller J, Jarzabek-Müller A, Bußler H, Gossner MM (2014) Hollow Beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Anim Conserv 17:154–162

Nilsson SG, Baranowski R (1997) Habitat predictability and the occurrence of wood beetles in old-growth Beech forests. Ecography 20:491–498

Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a Spruce forest in Southern Norway. Biodivers Conserv 5:75–100

Oleksa A, Chybicki IJ, Gawroński R, Svensson GP, Burczyk J (2013) Isolation by distance in saproxylic beetles May increase with niche specialization. J Insect Conserv 17:219–233

Oleksa A, Chybicki IJ, Larsson MC, Svensson GP, Gawroński R (2015) Rural avenues as dispersal corridors for the vulnerable saproxylic beetle *Elater ferrugineus* in a fragmented agricultural landscape. J Insect Conserv 19:567–580

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R Language. Bioinformatics 20:289–290

Percel G, Laroche F, Bouget C (2019) The scale of saproxylic beetles response to landscape structure depends on their habitat stability. Landscape Ecol 34:1905–1918

Quinto J, Micó E, Martínez-Falcón AP, Galante E, de los Angeles Marcos-Garcia M (2014) Influence of tree Hollow characteristics on the diversity of saproxylic insect guilds in Iberian mediterranean woodlands. J Insect Conserv 18:981–992

R Core Team (2024) R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91

Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126:363–370

Ranius T, Niklasson M, Berg N (2009a) Development of tree hollows in pedunculate oak (*Quercus robur*). For Ecol Manag 257:303–310

Ranius T, Svensson GP, Berg N, Niklasson M, Larsson MC (2009b) The successional change of Hollow Oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. Ann Zool Fenn 46:205–216

Ranius T, Johansson V, Fahrig L (2011) Predicting Spatial occurrence of beetles and pseudoscorpions in Hollow Oaks in southeastern Sweden. Biodivers Conserv 20:2027–2040

Ranius T, Johansson V, Schroeder M, Caruso A (2015) Relative importance of habitat characteristics at multiple Spatial scales for wood-dependent beetles in boreal forest. Landscape Ecol 30:1931–1942

Ries M, Balzer S, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Matzke-Hajek G (2021) Rote liste gefährdeter tiere, Pflanzen und Pilze Deutschlands, band 5: wirbellose tiere (Teil 3). – Münster (Landwirtschaftsverlag). – Naturschutz Und Biologische Vielfalt 70:165–186

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package ‘MASS’. CRAN R 538:113–120

Rüther C, Walentowski H (2008) Tree species composition and historic changes of the central European Oak/beech region. In: Floren A, Schmidl J (eds) Canopy arthropod research in Europe. Bioform, Nürnberg, pp 61–88

Schauer B, Bong J, Popp C, Obermaier E, Feldhaar H (2018a) Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. Basic Appl Ecol 32:26–38

Schauer B, Steinbauer MJ, Vailshery LS, Müller J, Feldhaar H, Obermaier E (2018b) Influence of tree Hollow characteristics on saproxylic beetle diversity in a managed forest. Biodivers Conserv 27:853–869

Schmidl J, Büche B (2018) Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick (Stand Sept. 2011). *Naturschutz und biologische Vielfalt* 70

Seibold S, Brandl R, Buse J, Hothorn T, Schmidl J, Thorn S, Müller J (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv Biol 29:382–390

Seibold S, Bässler C, Brandl R, Fahrig L, Förster B, Heurich M, Hothorn T, Scheipl F, Thorn S, Müller J (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology 98:1613–1622

Shepherd UL, Brantley SL (2005) Expanding on Watson’s framework for classifying patches: when is an Island not an Island? J Biogeogr 32:951–960

Siitonen J (2012) Microhabitats. In: Stokland JN, Siitonen J, Jonsson BG (eds) Biodiversity in dead wood. Cambridge University Press, Cambridge, pp 150–182

Speight MCD (1989) Saproxylic invertebrates and their conservation. Council of Europe. Nat Environ Ser 42:1–79

Stevens VM, Whitmee S, Le Galliard JF, Clobert J, Böhning-Gaese K, Bonte D, Brändle M, Dehling DM, Hof C, Trochet A, Baguette M (2014) A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecol Lett 17:1039–1052

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge

Sverdrup-Thygeson A, Gustafsson L, Kouki J (2014) Spatial and Temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodivers Conserv 23:513–535

Sverdrup-Thygeson A, Skarpaas O, Blumentrath S, Birkemoe T, Evju M (2017) Habitat connectivity affects specialist species richness more than generalists in veteran trees. For Ecol Manag 403:96–102

Thorn S, Seibold S, Leverkus AB, Michler T, Müller J, Noss RF, Stork N, Vogel S, Lindenmayer DB (2020) The living dead: acknowledging life after tree death to stop forest degradation. Front Ecol Environ 18:505–512

Traylor CR, Ulyshen MD, McHugh JV (2023) Forest age drives saproxylic beetle biodiversity in the southeastern united States. Biol Conserv 285:110238

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batary P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685

Ulyshen MD (2016) Wood decomposition as influenced by invertebrates. Biol Rev 91:70–85

Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301

Vogel S, Bussler H, Finnberg S, Müller J, Stengel E, Thorn S (2021) Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. Insect Conserv Divers 14:132–143

Wetherbee R, Birkemoe T, Skarpaas O, Sverdrup-Thygeson A (2020) Hollow Oaks and beetle functional diversity: significance of surroundings extends beyond taxonomy. Ecol Evol 10:819–831

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ORIGINAL ARTICLE

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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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Bastian Schauer and Benjamin Henneberg these authors are Co-first authors.

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

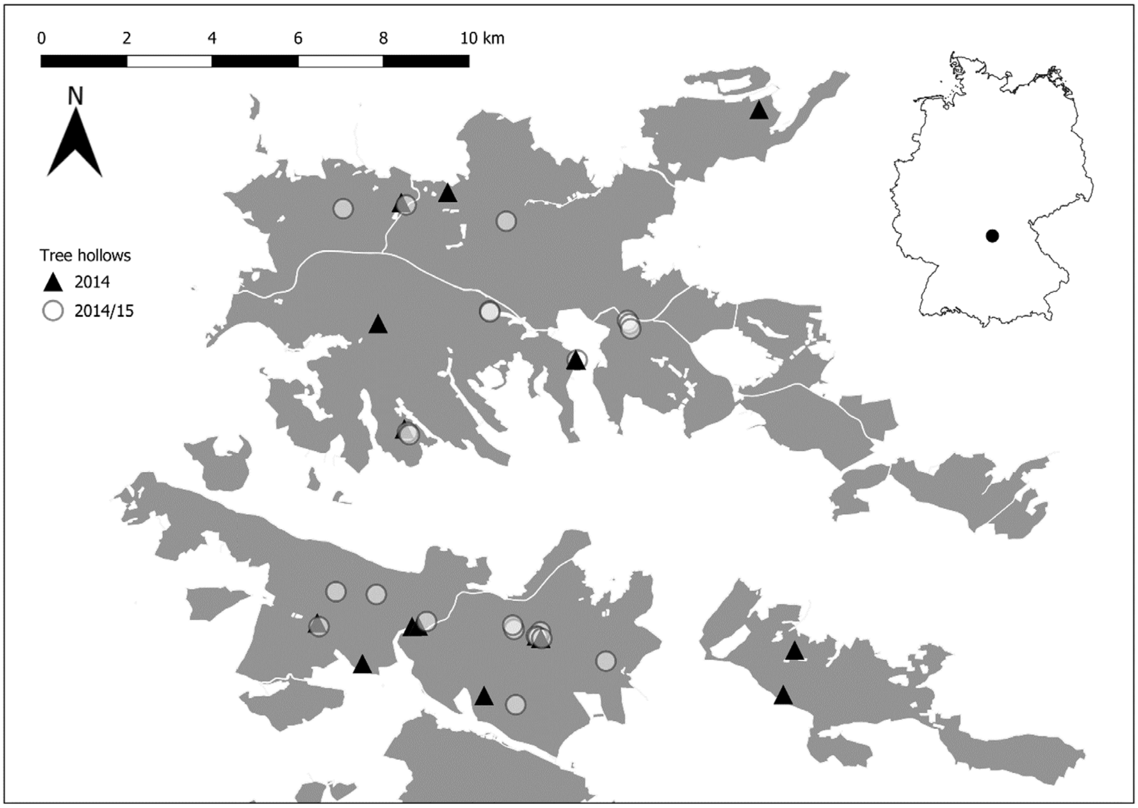

**FIGURE 1** Location of all 40 sampled tree hollows in the forestry department of Ebrach (Bavaria, Germany). Triangles represent tree hollows sampled in 2014 and circles represent tree hollows sampled in 2014 and 2015. Grey area indicates part of the forest district of Ebrach.

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

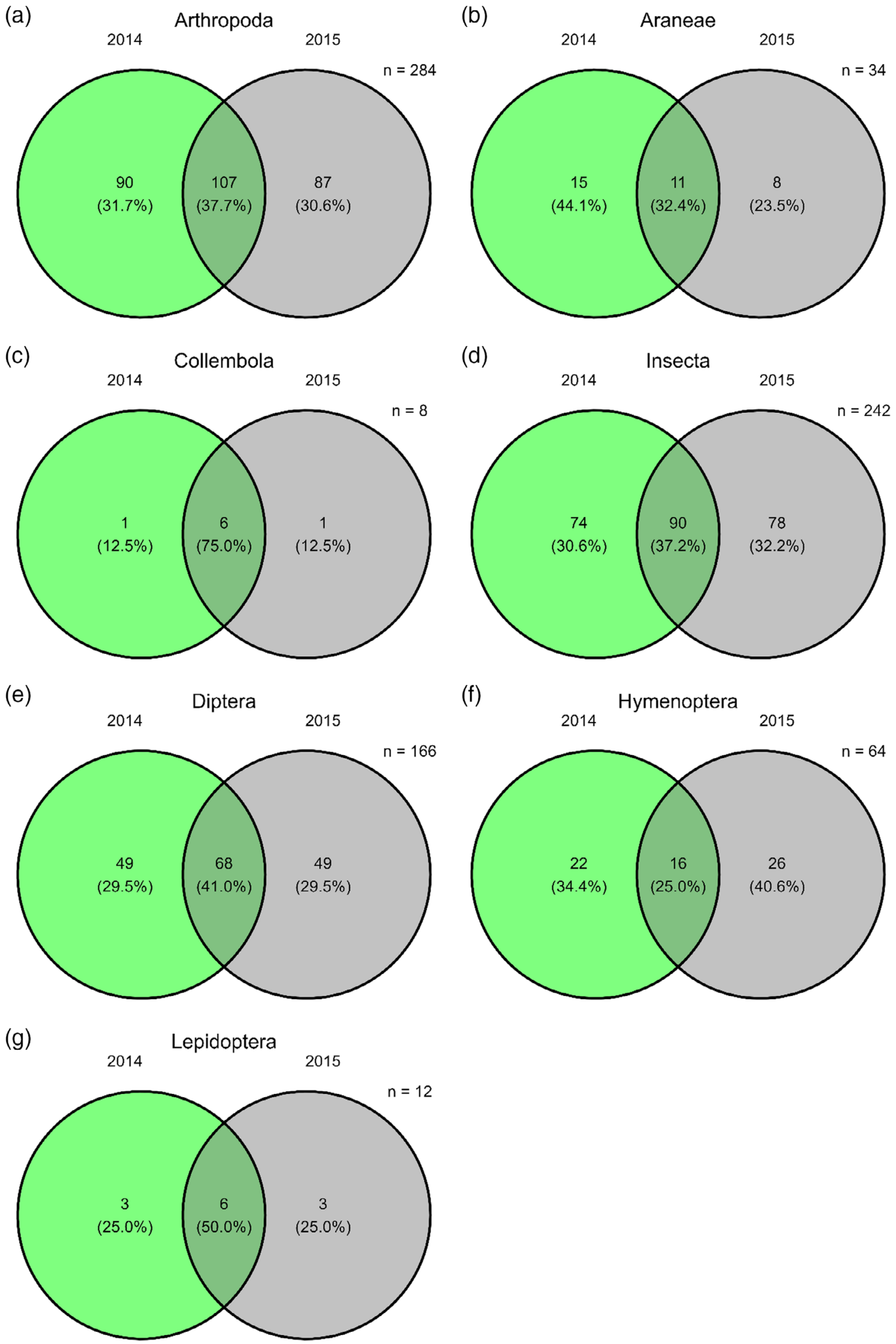

**FIGURE 2** Species numbers of arthropods sampled from emergence traps of 40 tree hollows in beech trees in 2014 and 23 tree hollows in 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera.

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.

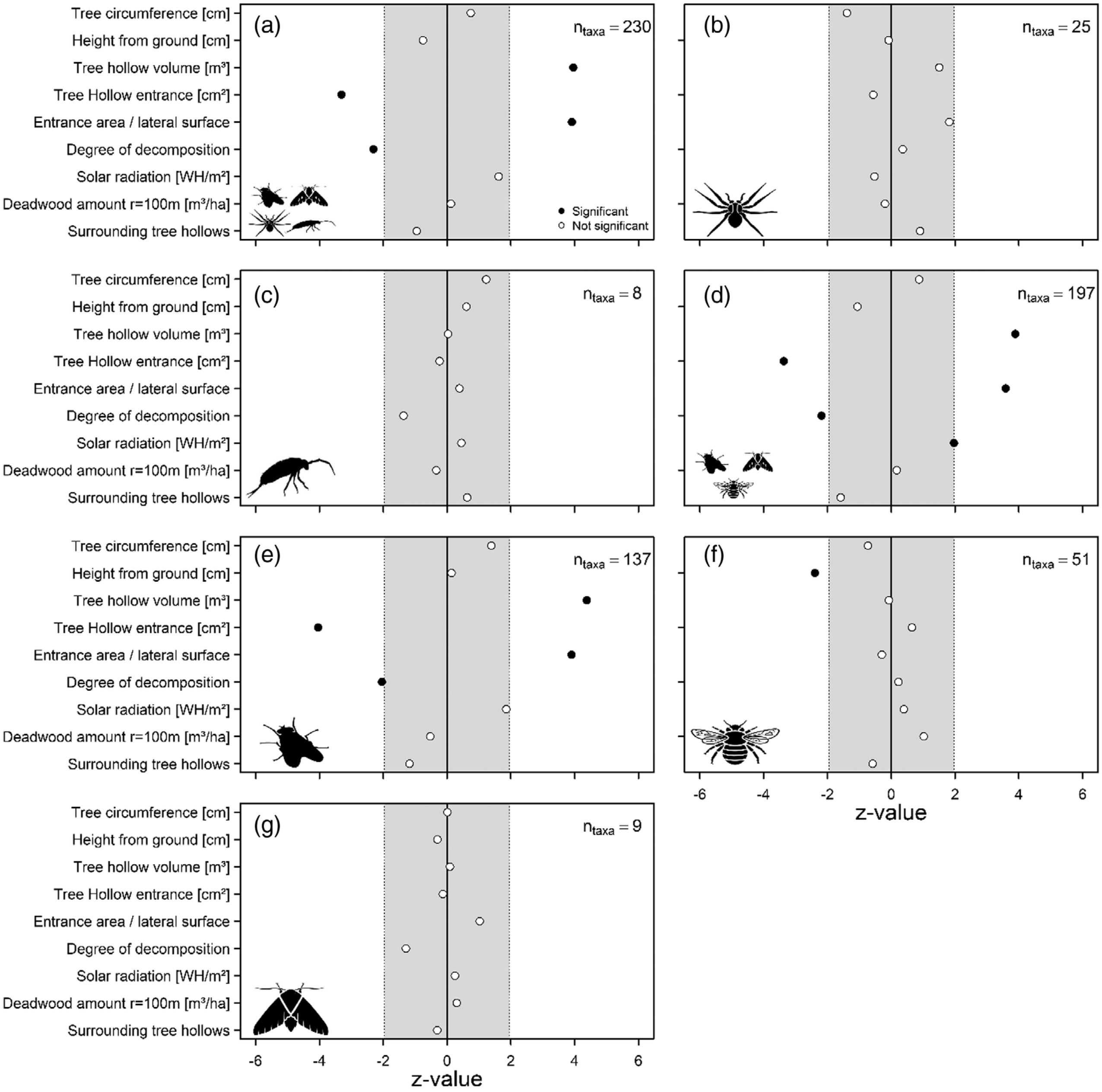

**FIGURE 3** α-diversity of arthropod samples collected with emergence traps of a subset of 23 tree hollows in beech trees pooled from 2014 and 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera. Grey area represents significance borders ($p < 0.05$), 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.

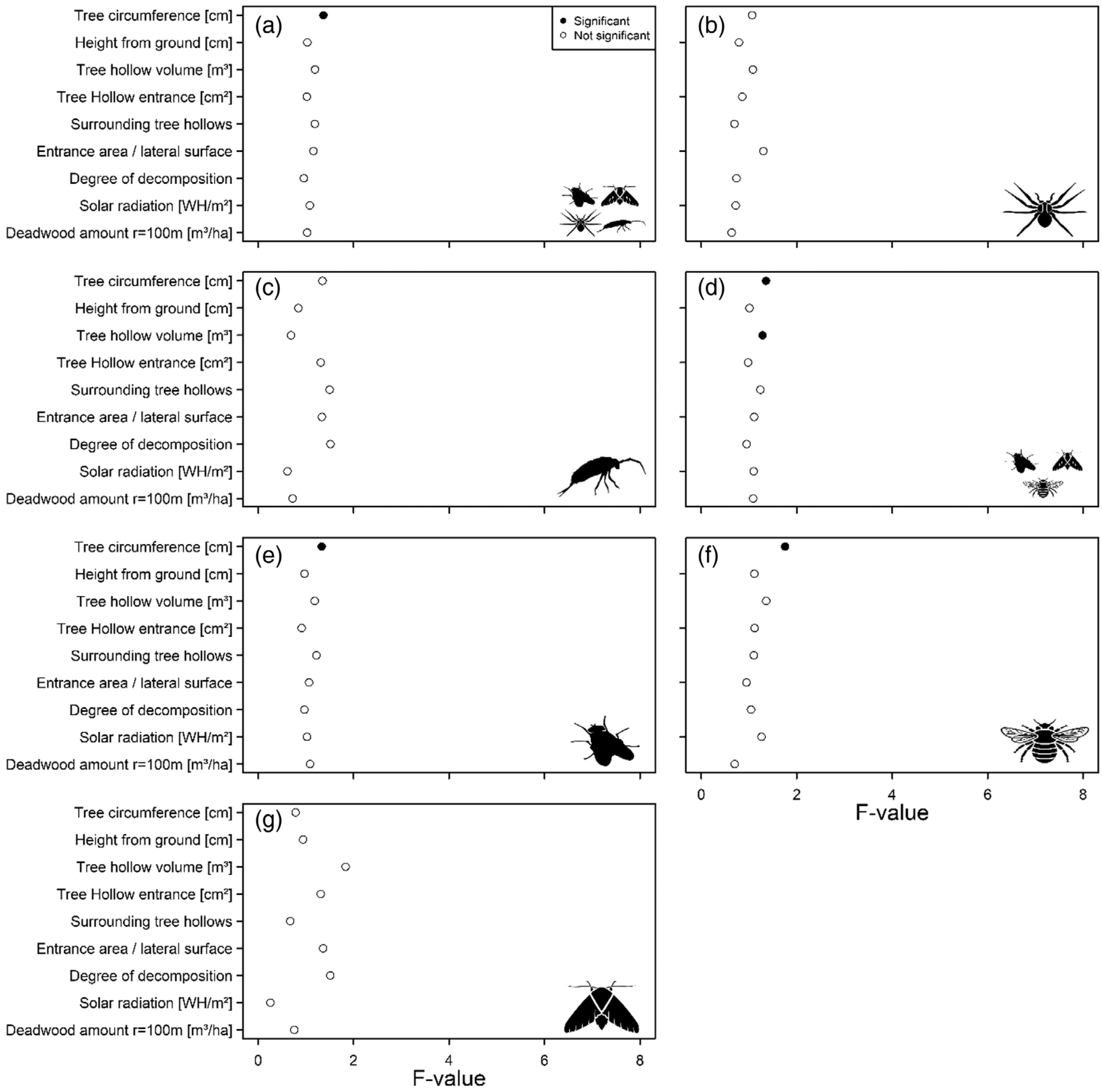

**FIGURE 4** β -diversity of arthropod samples collected with emergence traps of a subset of 23 tree hollows in beech trees pooled from 2014 and 2015 of (a) Arthropoda, (b) Araneae, (c) Collembola, (d) Insecta, (e) Diptera, (f) Hymenoptera and (g) Lepidoptera. Grey area represents significance borders ($p < 0.05$), 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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## REFERENCES

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J. et al. (2013) Genbank. *Nucleic Acids Research*, 41, 36–42.

Berisford, C.W. (2011) Parasitoids of the southern pine beetle. In: Coulson, R.N. & Klepzig, K.D. (Eds.) *Southern pine beetle II*. GTR SRS-140, Asheville, NC, USA: Southern Research Station, pp. 129–139.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K. et al. (2007) Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution*, 22(3), 148–155. Available from: https://doi.org/10.1016/j.tree.2006.11.004

Blakely, T.J., Harding, J.S. & Didham, R.K. (2012) Distinctive aquatic assemblages in water-filled tree holes: a novel component of freshwater biodiversity in New Zealand temperate rainforests. *Insect Conservation and Diversity*, 5, 202–212.

Bogusch, P. & Horák, J. (2018) Saproxylic bees and wasps. In: Ulyshen, M.-D. (Ed.) *Saproxylic insects: diversity, ecology and conservation*. Cham: Springer, pp. 217–235.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. et al. (2009) Generalized linear mixed models. A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. Available from: https://doi.org/10.1016/j.tree.2008.10.008

Braccia, A. & Batzer, D.P. (2008) Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats. *Canadian Journal of Forest Research*, 38, 2697–2704.

Darío Hernandes Córdoba, O., Torres-Romero, E.J., Villalobos, F., Chapa-Vargas, L. & Santiago-Alarcon, D. (2024) Energy input, habitat heterogeneity and host specificity drive avian haemosporidian diversity at continental scales. *Proceedings of the Royal Society B*, 291, 20232705.

Floren, A. & Schmidl, J. (2008) Introduction: canopy arthropod research in Europe. In: Floren, A. & Schmidl, J. (Eds.) *Canopy arthropod research in Europe*. Nürnberg: Bioform Entomology, pp. 13–20.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H. et al. (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, 6, 8568. Available from: https://doi.org/10.1038/ncomms9568

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D. et al. (2016) Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, 540(7632), 266–269. Available from: https://doi.org/10.1038/nature20575

Gouix, N. & Brustel, H. (2012) Emergence trap, a new method to survey *Limoniscus violaceus* (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation*, 21, 421–436.

Goulson, D. (2003) *Bumblebees: their behaviour and ecology*. USA: Oxford University Press, p. 235.

Graf, M., Seibold, S., Gossner, M.M., Hagge, J., Weiß, I., Bässler, C. et al. (2022) Coverage based diversity estimates of facultative saproxylic species highlight the importance of deadwood for biodiversity. *Forest Ecology and Management*, 517, 11–41.

Harrell, F., Jr. (2024) Hmisc: Harrell Miscellaneous. R Package Version 5.2-1. https://CRAN.R-project.org/package=Hmisc

Hausmann, A., Godfray, H.C.J., Huemer, P., Mutanen, R., Rougerie, R., van Nieukerken, E.J. et al. (2013) Genetic patterns in European geometrid moths revealed by the barcode index number (BIN) system. *PLoS One*, 8(12), e84518. Available from: https://doi.org/10.1371/journal.pone.0084518

Hausmann, A., Segerer, A.H., Greifenstein, T., Knubben, J., Morinière, J., Bozicevic, V. et al. (2020) Toward a standardized quantitative and qualitative insect monitoring scheme. *Ecology and Evolution*, 10, 4009–4020.

Henneberg, B., Bauer, S., Birkenbach, M., Mertl, V., Steinbauer, M.J., Feldhaar, H. et al. (2021) Influence of tree hollow characteristics and forest structure on saproxylic beetle diversity in tree hollows in managed forests in a regional comparison. *Ecology and Evolution*, 11, 17973–17999.

Hernández-Corral, J., García-López, A., Ferrández, M.Á. & Micó, E. (2021). Physical and biotic factors driving the diversity of spider assemblages in tree hollows of Mediterranean Quercus forests. *Insect Conservation and Diversity*, 14(4), 515–526. Portico. Available from: https://doi.org/10.1111/icad.12483

Hilszczański, J. (2018) Ecology, diversity and conservation of saproxylic hymenopteran parasitoids. In: Ulyshen, M.D. (Ed.) *Saproxylic insects: diversity, ecology and conservation*. Cham: Springer, pp. 193–216.

Hövemeyer, K. & Schauermann, J. (2003) Succession of Diptera on dead beech wood: a 10-year study. *Pedobiologia*, 47(1), 61–75. Available from: https://doi.org/10.1078/0031-4056-00170

Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A. et al. (2018) Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology Letters*, 21, 763–778.

Ji, Y., Ashton, L., Pedley, S.M., Edwards, D.P., Tang, Y., Nakamura, A. et al. (2013) Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology Letters*, 16(10), 1245–1257. Available from: https://doi.org/10.1111/ele.12162

Jonsell, M. (2004) Old park trees: a highly desirable resource for both history and beetle diversity. *Arboriculture & Urban Forestry*, 30, 238–244.

Kitching, R.L. (1971) An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *Journal of Animal Ecology*, 40(2), 281–302. Available from: https://doi.org/10.2307/3247

Kitching, R.L. (2000) *Food webs and container habitats: the natural history and ecology of phytotelmata*. Cambridge: Cambridge University Press, p. 431.

Legendre, P. & Anderson, M.J. (1999) Distance-based redundancy analysis. Test multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69, 1–24.

Lindenmayer, D.B., Laurance, W.F. & Franklin, J.F. (2012) Global decline in large old trees. *Science*, 338, 1305–1306.

Lindman, L., Öckinger, E. & Ranius, T. (2023) Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*. *Ecological Entomology*, 48, 112–126.

Lofroth, E. (1998) The dead wood cycle. In: Voller, J. & Harrison, S. (Eds.) *Conservation biology principles for forested landscapes*. Vancouver: UBC Press, pp. 185–214.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, 42, 594–598.

Majumder, J., Goswami, R. & Agarwala, B.K. (2011) A preliminary study on the insect community of phytotelmata: an ephemeral ecosystem in Tripura, Northeast India. *NeBIO*, 2, 27–31.

Michener, C.D. (2007) *The bees of the world*, 2nd edition. Baltimore and London: The Johns Hopkins University Press, p. 992.

Micó, E., García-López, A., Sánchez, A., Juárez, M. & Galante, E. (2015). What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? *Journal of Insect Conservation*, 19(1), 141–153. Available from: https://doi.org/10.1007/s10841-015-9754-9

Micó, E. (2018) Saproxylic insects in tree hollows. In: Ulyshen, M.D. (Ed.) *Saproxylic insects: diversity, ecology and conservation*. Cham: Springer, pp. 693–727.

Morales-Hidalgo, D., Oswalt, S.N. & Somanathan, E. (2015) Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the global Forest resources assessment 2015. *Forest Ecology and Management*, 352, 68–77. Available from: https://doi.org/10.1016/j.foreco.2015.06.011

Müller, J., Jarzabek-Müller, A., Bussler, H. & Gossner, M.M. (2014) Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation*, 17, 154–162.

Müller, J., Mitesser, O., Cadotte, M.W., van der Plas, F., Mori, A.S., Ammer, C. et al. (2023) Enhancing the structural diversity between forest patches – a concept and real-world experiment to study biodiversity, multifunctionality and forest resilience across spatial scales. *Global Change Biology*, 29, 1437–1450.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C. et al. (2020) Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, 129, 1579–1588.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37, 191–203.

Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M. et al. (2014) *European red list of bees*. Brussels: Office of the European Union, p. 86.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2016) Vegan: community ecology package. Version 2.5-6. https://CRAN.R-project.org/package=vegan

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19, 18–24.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P.P., Avon, C., Bernhardt-Römermann, M. et al. (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101–112. Available from: https://doi.org/10.1111/j.1523-1739.2009.01399.x

Porter, T.M. & Hajibabaei, M. (2018) Automated high throughput animal CO1 metabarcode classification. *Scientific Reports*, 8(1), 4226. Available from: https://doi.org/10.1038/s41598-018-22505-4

Quinto, J., Micó, E., Martìnez-Falcón, A.P., Galante, E. & de los Angeles Marcos-Garcìa, M. (2014) Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *Journal of Insect Conservation*, 18, 981–992.

R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Ranius, T. (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation*, 103, 85–91.

Ranius, T., Gibbons, P. & Lindenmayer, D. (2024) Habitat requirements of deadwood-dependent invertebrates that occupy tree hollows. *Biological Reviews*, 99, 2022–2034.

Ratnasingham, S. & Hebert, P.D. (2007) BOLD: the barcode of life data system. *Molecular Ecology Notes*, 7, 355–364. Available from: http://www.barcodinglife.org

Ratnasingham, S. & Hebert, P.D. (2013) A DNA-based registry for all animal species: the barcode index number (BIN) system. *PLoS One*, 8(7), e66213. Available from: https://doi.org/10.1371/journal.pone.0066213

Reemer, M. (2005) Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae). *Journal of Insect Conservation*, 9(1), 49–59. Available from: https://doi.org/10.1007/s10841-004-6059-9

Ricarte, A., Jover, T., Marcos-García, M.A., Micó, E. & Brustel, H. (2009) Saproxylic beetles (Coleoptera) and hoverflies (Diptera: Syrphidae) from a Mediterranean forest: towards a better understanding of their biology for species conservation. *Journal of Natural History*, 43, 583–607.

Rolls, R.J., Deane, D.C., Johnson, S.E., Heino, J., Anderson, M.J. & Ellingsen, K.E. (2023) Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews*, 98, 1388–1423.

Salis, R., Sunde, J., Gubonin, N., Franzén, M. & Forsman, A. (2024) Performance of DNA metabarcoding, standard barcoding and morphological approaches in the identification of insect biodiversity. *Molecular Ecology Resources*, 24, e14018.

Sánchez-Galván, I.R., Quinto, J., Micó, E., Galante, E. & Marcos-García, M.A. (2014) Facilitation among saproxylic insects inhabiting tree hollows in a Mediterranean forest: the case of cetoniids (Coleoptera: Cetoniidae) and syrphids (Diptera: Syrphidae). *Environmental Entomology*, 43, 336–343.

Schauer, B., Steinbauer, M.J., Vailshery, L.S., Müller, J., Feldhaar, H. & Obermaier, E. (2018) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation*, 27, 853–869.

Schauer, B., Thorn, S., Blaschke, M. & Kudernatsch, T. (2023) Conversion of pure spruce to mixed spruce beech stands: effects on alpha and beta diversity of multiple taxonomic groups. *Forest Ecology and Management*, 545, 121297. Available from: https://doi.org/10.1016/j.foreco.2023.121297

Schmidl, J., Sulzer, P. & Kitching, R.L. (2008) The insect assemblage in water-filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physiochemical factors. *Hydrobiologia*, 598, 285–303.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M.D. et al. (2016) Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, 204, 181–188.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S. et al. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53, 934–943.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. et al. (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29, 382–390.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.

Siitonen, J. (2012) Microhabitats. In: Stokland, J.N., Siitonen, J. & Jonsson, B.G. (Eds.) *Biodiversity in dead wood*. Cambridge: Cambridge University Press, pp. 150–182.

Siitonen, J. & Ranius, T. (2015) The importance of veteran trees for saproxylic insects. In: Kirby, K.J. & Watkins, C. (Eds.) *Europe's changing woods and forests: from wildwood to managed landscapes*. Oxfordshire: CABI, pp. 140–153.

Smolis, A., Zając, K., Tyszecka, K. & Kadej, M. (2023) Why is the hermit beetle so rare in central European managed forests? Habitat requirements of the forest population of *Osmoderma barnabita*. *Forest Ecology and Management*, 548, 121407.

Sobek, S., Tscharntke, T., Scherber, C., Schiele, S. & Steffan-Dewenter, I. (2009) Canopy vs. understory: does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecology and Management*, 258, 609–615.

Speight MCD. (1989) Saproxylic invertebrates and their conservation. Council of Europe, Nature and Environment Series 42, Strasbourg. Cham.

Srivastava, D.S. & Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, 152, 510–529.

Stokland, J.N. & Siitonen, J. (2012) Mortality factors and decay succession. In: Stokland, J.N., Siitonen, J. & Jonsson, B.G. (Eds.) *Biodiversity in dead wood*. Cambridge: Cambridge University Press, pp. 110–149.

Sverdrup-Thygeson, A., Skarpaas, O. & Ødegaard, F. (2010) Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation*, 19, 837–852.

Taberlet, P., Coissac, E., Hajibabaei, M. & Rieseberg, L.H. (2012) Environmental DNA. *Molecular Ecology*, 21, 1789–1793.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. et al. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79–92.

Thiele, R. (2005) Phenology and nest site preferences of wood-nesting bees in a Neotropical lowland rain forest. *Studies on Neotropical Fauna and Environment*, 40, 39–48.

Ulyshen, M.D. (2018) Saproxylic Diptera. In: Ulyshen, M.D. (Ed.) *Saproxylic insects: diversity, ecology and conservation*. Cham: Springer, pp. 167–192.

Vanderwel, M.C., Malcolm, J.R., Smith, S.M. & Islam, N. (2006) Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *Forest Ecology and Management*, 225, 190–199.

Wermelinger, B. (2004) Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *Forest Ecology and Management*, 202(1-3), 67–82. Available from: https://doi.org/10.1016/j.foreco.2004.07.018

Westerfelt, P., Widenfalk, O., Lindelöw, Å., Gustafsson, L. & Weslien, J. (2015) Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conservation and Diversity*, 8(6), 493–504. Available from: https://doi.org/10.1111/icad.12128

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), 279–338. Available from: https://doi.org/10.2307/1943563

Yanovlak, S.P. (2001) The macrofauna of water-filled tree holes on Barro Colorado Island, Panama. *Biotropica*, 33, 110–120.

Young, M.R. & Hebert, P.D.N. (2022). Unearthing soil arthropod diversity through DNA metabarcoding. PeerJ, 10, e12845. Portico. Available from: https://doi.org/10.7717/peerj.12845

Yu, D.W., Ji, Y., Emerson, B.C., Wang, X., Ye, C., Yang, C. et al. (2012) Biodiversity soup. Metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. *Methods in Ecology and Evolution*, 3, 613–623.

## 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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# Discussion

## Factors that influence diversity of saproxylic beetles in tree hollows at small spatial scales (manuscript 1)

In the first part of this study, I examined the influence of characteristics of tree hollows, hollow-bearing trees and local forest structure on species richness of hollow-dwelling saproxylic beetles in a regional comparison between the three study regions Ebrach, Fichtelberg and Kelheim (Henneberg et al. 2021, manuscript 1). The three study regions were characterized by different forest structure (tree-species composition, amount and distribution of dead wood) and management regime. As a new method of analysis I used forest inventory data that are regularly collected by the Bavarian state forest authorities (BaySF) to investigate the influence of forest structure at spatial scales of 50 m - 500 m around the focal tree hollows on saproxylic beetle diversity in the hollows. By conducting a regional comparison between the three study regions I set out to validate the relationships between local characteristics of tree hollows or hollow-bearing trees and species richness of saproxylic beetles in the hollows that Schauer et al. (2018b) obtained in the Ebrach forestry (Steigerwald). By analyzing parameters of forest structure at spatial scales of 50 m - 500 m around the focal tree hollows using forest inventory data as a new method of analysis, I expanded the spatial scope of the study.

I was able to confirm some reoccurring patterns of saproxylic beetle diversity in tree hollows, namely the positive effect of a large entrance area of tree hollows on species richness of hollow-dwelling saproxylic beetles (see also Ranius 2002; Ranius et al. 2009a, 2009b; Quinto et al. 2014, 2015; Schauer et al. 2018b), the positive effect of a large hollow volume on threatened species (see also Ranius & Jansson 2000; Sverdrup-Thygeson et al. 2010; Quinto et al. 2014), the positive effect of temperature within the hollows (see also Ranius & Nilsson 1997; Lindhe et al. 2005; Koch Widerberg et al. 2012; Müller et al. 2015a), the negative effect of height of the hollow entrance above ground (see also Quinto et al. 2014; Taylor & Ranius 2014; Schauer et al. 2018b), or the negative effect of stage of decomposition of the wood mold within the tree hollows (see also Stokland & Siitonen 2012; Sverdrup-Thygeson et al. 2014; Schauer et al. 2018b). Most of these findings underpin the notion that saproxylic beetles are positively affected by tree hollow characteristics that reflect a large amount of resources (large hollow volume) or a stable and warm microclimate (large entrance area, high temperature). A stable microclimate is probably a key factor why some species of saproxylic beetles are specialized in tree hollows (Ranius et al. 2024). However, the comparison of the three study regions Ebrach, Fichtelberg and Kelheim with differing forest structure (tree-species composition, amount and distribution of dead wood) showed the large influence of the surrounding environment and landscape for the various interactions between tree hollow parameters or parameters of forest structure at 50 m - 500 m around the focal tree hollows and species richness of hollow-dwelling saproxylic beetles. It has been suggested that the influence of various parameters of tree hollows or forest structure on species richness and community structure within tree hollows was changing between different species groups, environments, landscapes and climate zones (Schauer 2018; Müller et al. 2020). That notion was confirmed by the results obtained in the regional comparison of the three forest regions as the influence of tree hollow parameters or parameters of surrounding forest structure on saproxylic beetle species richness in the hollows varied substantially between the different forest regions (Henneberg et al. 2021, manuscript 1). As a new method of analysis I used forest inventory data that are regularly collected by the BaySF in all Bavarian state forestries and assessed the amount of dead wood and the diameter of deciduous trees (as a proxy for age structure) at spatial scales of 50 m - 500 m around the focal tree hollows. Additionally, in the mostly coniferous Fichtelberg study region, the proportion of beech trees around the focal tree hollows was assessed.

Dead wood amount in the surrounding forest area has been shown in numerous studies to be an important parameter that can positively influence saproxylic beetle species richness (Martikainen et al. 2000; Grove 2002; Müller et al. 2008; Sverdrup-Thygeson et al. 2010; Gossner et al. 2013; Müller et al. 2015a). Accordingly, in the Ebrach study region a significant positive relationship between dead wood amount in the surrounding forest area at spatial scales of 50 m and 100 m around the focal tree hollows and saproxylic beetle species richness in the hollows was detected (Henneberg et al. 2021, manuscript 1). The finding that dead wood amount in Ebrach only affected species richness of hollow-dwelling saproxylic beetles at small spatial scales of 50 m and 100 m around the focal tree hollows may be due to the assumed limited dispersal ability of many saproxylic beetle species living in tree hollows (Jonsson 2012; Percel et al. 2019; see also the following chapter on the influence of the surrounding landscape at larger spatial scales). In the Fichtelberg and Kelheim study regions this relationship was not observed. The Ebrach study region is characterized by the highest proportion of deciduous trees out of the three study regions. Therefore, dead wood in the Ebrach study region is likely to be dead wood of deciduous trees. Most saproxylic beetle species are assumed to be either specialized in dead wood of deciduous or coniferous trees (Stokland & Siitonen 2012; Milberg et al. 2014; Vogel et al. 2021). Since only species that inhabit tree hollows in beech trees were examined in this study, this may explain why Ebrach was the only study region where the amount of dead wood in the near surroundings of the focal tree hollows had a significant positive effect on saproxylic beetle species richness in the hollows. This finding shows that in forest regions with a high proportion of deciduous trees, the amount of dead wood up to a radius of 100 m around the focal tree hollows can positively affect saproxylic beetle species richness in the hollows. In forest regions with low proportions of deciduous trees, in contrast, the amount of dead wood in the near surroundings of tree hollows does not affect saproxylic beetle species richness in the hollows. Thus, total dead wood amount is not a sufficient indicator of species richness of hollow-dwelling saproxylic beetles, and tree-species composition in the surrounding forest area as well as type of dead wood (standing or downed, volume, stage of decomposition) should always be integrated to allow a better prediction of saproxylic biodiversity (Lassauce et al. 2011; Seibold & Thorn 2018).

Another example showcasing how differences in the surrounding environment or landscape affect the parameters that influence tree hollow assemblages was obtained in the mostly coniferous Fichtelberg study region. Characterized by the lowest proportion of deciduous trees out of the three study regions, the only parameter of forest structure that influenced total species richness of hollow-dwelling saproxylic beetles in beech trees in the Fichtelberg study region was the proportion of beech trees up to a radius of 100 m around the focal tree hollows (Henneberg et al. 2021, manuscript 1). This result shows that in a forest region where deciduous trees with potentially suitable tree hollow habitats are very limited, the number of potential habitat trees in the near surroundings of tree hollows is the most important parameter influencing saproxylic beetle species richness in the hollows, and the quality of the habitat (characteristics of the tree hollow itself) might be of secondary importance (Henneberg et al. 2021, manuscript 1). The fact that in the Fichtelberg study region neither the amount of dead wood around the focal tree hollows nor any of the other investigated parameters of forest structure besides the proportion of beech trees in the surroundings had any significant effect on saproxylic beetle species richness in the hollows again shows that the importance of parameters of tree hollows or forest structure for saproxylic assemblages in the hollows depends on the surrounding environment or landscape, in this case the tree-species composition in the surrounding forest area.

The climate zone where the examined tree hollows are located is another variable that may affect the parameters that influence species assemblages in tree hollows. For example, Carpaneto et al. (2010) have shown that occurrence patterns of *Osmoderma eremita*, a threatened flagship saproxylic beetle species for the conservation of tree hollow assemblages in Europe, were positively affected by higher temperatures in northern Europe, but negatively affected by higher temperatures in southern Europe. Since the three study regions in my study were all located in central Europe, characterized by a colder climate than southern Europe, it is in accordance with Carpaneto et al. (2010) that total species richness of saproxylic beetles in Ebrach and of threatened species across all three study regions was positively affected by temperature inside the hollows (Henneberg et al. 2021, manuscript 1). A positive relationship between temperature and species richness of saproxylic beetles has been reported from central Europe before (Müller et al. 2015a; Schauer et al. 2018), especially for threatened saproxylic beetle species (Lindhe et al. 2005; Koch Widerberg et al. 2012). Thus, Müller et al. (2015) proposed that conservationists, forest managers and ecologists should pay more attention to the climate gradient as one fundamental driver of saproxylic beetle diversity. Another important variable that affects the parameters that influence species composition in tree hollows is the species group that is being researched (see the chapter on non-beetle saproxylic taxa living in tree hollows (manuscript 3)).

In summary, it can be stated that there are parameters of tree hollows or forest structure that positively affect saproxylic beetle species richness in tree hollows (e.g., a large hollow volume, a large hollow entrance, a warm microclimate, an early stage of wood mold decomposition, large amounts of dead wood of deciduous trees) (Henneberg et al. 2021; manuscript 1), but the significance of these effects highly depends on context. Either with regard to the surrounding environment (e.g., the tree-species composition around the focal tree hollows) or with regard to the climatic conditions (see Chiari et al. 2013). In my study, the influence of forest structure on saproxylic beetle species richness in tree hollows was examined at spatial scales of 30 m - 500 m in the three study regions, however, significant results were obtained only for spatial scales of 50 m and 100 m in the mostly deciduous Ebrach forest region (positive influence of the amount of dead wood) and in the mostly coniferous Fichtelberg forest region (positive influence of the proportion of beech trees) (Henneberg et al. 2021; manuscript 1). Using forest inventory data as a new method of analysis has proven to be a valuable method as these detailed forest data are readily available and do not have to be labor-intensively recorded in the field.

### Influence of the surrounding landscape at larger spatial scales (manuscript 2)

Besides characteristics of tree hollows, hollow trees and local forest structure, the landscape surrounding the focal tree hollows at different spatial scales influences occurrence patterns of saproxylic beetles in tree hollows (Økland et al. 1996; Franc et al. 2007; Müller & Gossner 2010; Sverdrup-Thygeson et al. 2014; Ranius et al. 2015; Ranius et al. 2024). However, studies of landscape effects at larger spatial scales on saproxylic assemblages in tree hollows are still scarce (Sverdrup-Thygeson et al. 2014; Ranius et al. 2024). Therefore, in the second part of this study we widened the spatial scale by utilizing satellite imagery to analyze the landscape surrounding the focal tree hollows at radii of 300 m - 5000 m (Henneberg et al. 2025; manuscript 2). We set out to gain a better understanding of the interactions between landscape composition at different spatial scales around the tree hollows and diversity of saproxylic beetles in the hollows.

We found that the surrounding landscape composition, namely the proportion of potentially suitable habitat surrounding the focal tree hollows, did not have an effect on total species richness of saproxylic beetles in the hollows, but it did positively affect species richness of threatened saproxylic beetle species in the Ebrach study region at spatial scales of 300 m - 5000 m around the focal tree hollows and in the Fichtelberg study region at spatial scales of 300 m - 4000 m around the focal tree hollows (Henneberg et al. 2025; manuscript 2). Thus, threatened saproxylic beetle species seem to react more sensitively to the surrounding landscape composition compared to total species richness of saproxylic beetles. Since the proportion of threatened species is higher within highly specialized species groups - in Germany approx. 75% - 86% of tree hollow specialist species are threatened (Floren & Schmidl 2008

[86%]; Schmidl & Büche 2018 [75%]) - it can be inferred that saproxylic beetle species that are dependent on the occurrence of tree hollows react more sensitively to the availability of potentially suitable habitat in the surroundings of the focal tree hollows compared to species that can also utilize other dead wood habitats. This finding is in line with the current doctrine in the literature which states that highly specialized saproxylic beetle species rely more on certain habitat conditions and resources (Müller et al. 2005; Gossner & Müller 2011) and are more threatened by habitat fragmentation (Sverdrup-Thygeson et al. 2017) compared to generalist species. This notion gets amplified by the assumption that tree hollow specialist species seem to possess rather low dispersal abilities as their required habitat is stable and long-lasting (Ranius & Hedin 2001; Hedin et al. 2008; Jonsson 2012; Oleksa et al. 2015; Percel et al. 2019). This assumption can be attributed to the "stability-dispersal model" which predicts that species specialized in stable habitats should have lower dispersal abilities than species associated with short-lived habitats (Percel et al. 2019). It has been shown for hollow-dwelling saproxylic beetles that they react more sensitively to the surrounding landscape at spatial scales of up to 1500 m radius compared to beetles in more short-lived dead wood habitats (Percel et al. 2019). Thus, I expected that threatened species, e.g., all of the tree hollow specialist species in my study, depend more on habitat availability within the surrounding landscape than generalist species (see also Götmark et al. 2011; Jacobsen et al. 2015). This expectation was confirmed as the proportion of potentially suitable habitat in the surrounding landscape positively affected species richness of threatened hollow-dwelling saproxylic beetles in Ebrach and Fichtelberg at spatial scales of 300 m - 5000 m around the focal tree hollows, but not total species richness (Henneberg et al. 2025; manuscript 2). This is an important insight for the planning of conservation measures as understanding scale dependency is crucial for the conservation of biodiversity (Müller & Gossner 2010; Tscharntke et al. 2012; Micó et al. 2013; Ranius et al. 2015) (see the following chapter on scale dependency of saproxylic beetles in tree hollows). Therefore, when lacking precise knowledge of dispersal distances of threatened saproxylic species, the spatial scale of conservation efforts in managed forests should be adapted to the lifetime of the target species' preferred habitat as species specialized in long-lasting habitats are assumed to have lower dispersal abilities than species associated with short-lived habitats (Percel et al. 2019; Henneberg et al. 2025; manuscript 2).

It has been proposed that human land use might filter saproxylic beetle species assemblages by selecting against species with particular morphological traits, e.g., through habitat fragmentation or ecological degradation of forests (Hagge et al. 2021). Therefore, we hypothesized that tree hollows that are located in small and isolated forest patches (e.g., in the Kelheim study region) or those isolated within a matrix of coniferous forest (e.g., in the Fichtelberg study region) would contain saproxylic beetle communities that shift towards species with a better dispersal ability, i.e., species showing morphological traits that facilitate dispersal, compared to species assemblages in large and well-connected deciduous forest stands (e.g., the Ebrach study region) (Henneberg et al. 2025; manuscript 2). This hypothesis was partly confirmed as we found significant relationships between the functional diversity index “functional richness” (FRic) regarding dispersal-associated morphological traits and surrounding habitat proportion in the Fichtelberg and Kelheim study regions. In Fichtelberg, where focal tree hollows were surrounded by a matrix of coniferous trees, morphological traits of hollow-dwelling saproxylic beetles shifted towards traits that facilitate dispersal (large body size, large wing length) (Henneberg et al. 2025; manuscript 2). Thus, it seems that saproxylic beetle assemblages in tree hollows that are surrounded by forest with a very limited availability of suitable tree hollows shift towards species with a good dispersal ability. Although there were generally fewer hollow-dwelling saproxylic beetle species in the mostly coniferous Fichtelberg study region compared to the other two study regions with higher proportions of deciduous trees, it could be inferred that these species were on average better dispersers and might be able to colonize isolated tree hollows in distant parts of the Fichtelberg forest region. In the Kelheim study region, however, a forest region characterized by small and isolated forest patches with agricultural open land and towns in between, dispersal-associated functional richness in tree hollows increased when there were low proportions of forest in the surroundings. Hence, it seems that these assemblages were comprised of saproxylic beetle species with good dispersal ability and species with more limited dispersal ability. Thus, some species in these assemblages may be inclined to disperse across open land while others are not. In large forest patches in the Kelheim study region, functional richness in the tree hollows decreased, presumably because the sufficient availability of suitable habitat in the surroundings did not select for good dispersal ability (Henneberg et al. 2025; manuscript 2). These findings show that isolation of tree hollows in terms of coniferous forest surrounding the focal deciduous hollow trees affects species assemblages in tree hollows differently than fragmentation of forest patches with open land in between. This leads to the assumption that some species of hollow-dwelling saproxylic beetles readily disperse across open land while others only disperse within forested areas (Henneberg et al. 2025; manuscript 2).

These results show that the influence of surrounding landscape composition, measured as proportion of suitable habitat surrounding the focal tree hollows at spatial scales of 300 m - 5000 m, is stronger for threatened saproxylic beetle species in tree hollows compared to total species richness, but depends on size and connectivity of habitat patches. On the one hand, it was shown that threatened saproxylic beetle species that are associated with limited dispersal abilities, will benefit from an increased habitat proportion in their surroundings (Henneberg et al. 2025; manuscript 2). On the other hand, habitat connectivity can be assumed to be a mediating factor mitigating the effect of surrounding habitat proportion on species assemblages in tree hollows because some species of saproxylic beetles seem to not readily disperse across open land. Therefore, these species may not be able to colonize tree hollows in isolated forest fragments.

## Scale dependency of saproxylic beetles in tree hollows

Despite an ever-growing body of literature on the ecology of saproxylic beetles in tree hollows we still have very limited knowledge of the relationships between saproxylic beetle diversity in tree hollows and characteristics of the surrounding forest structure and landscape structure at different spatial scales (Sverdrup-Thygeson et al. 2014; Ranius et al. 2024). A better understanding of the effect of these parameters at different spatial scales on hollow-dwelling saproxylic beetles could have significant consequences for the planning of forest management and conservation (Lindenmayer et al. 2008). To my knowledge this study is the first time that either interpolated forest inventory data (see Henneberg et al. 2021, manuscript 1) or the proportion of potentially suitable habitat in the surrounding landscape at different spatial scales (see Henneberg et al. 2025; manuscript 2) has been related to species richness or functional diversity of saproxylic beetles in tree hollows. Most studies that assessed relationships between saproxylic beetles' occurrence patterns in tree hollows and characteristics of the surrounding landscape examined the amount of dead wood in the surroundings (Müller et al. 2008; Sverdrup-Thygeson et al. 2010; Gossner et al. 2013; Müller et al. 2015a), the number of tree hollows in the surroundings (see Ranius et al. 2011; Musa et al. 2013; Pilskog et al. 2018) or the distance to potential dispersal sources (see Jansson et al. 2009; Kadej et al. 2016; Mestre et al. 2018). One study has been conducted that showed that the spatial scale at which characteristics of the surrounding landscape (number of tree hollows) had significant effects on hollow-dwelling saproxylic beetles was smaller compared to saproxylic beetles in more short-lived dead wood habitats (dead wood and polypore fungi), presumably because species specialized in long-lasting habitats have lower dispersal abilities than species associated with more short-lived habitats (Percel et al. 2019). Hollow-dwelling saproxylic beetles in that study were affected by the number of tree hollows in the surrounding landscape up to a radius of approx. 300 m (Percel et al. 2019). These findings are in line with the results of my study as I showed that the explanatory power of the statistical models was larger when local tree hollow characteristics or forest structure at small spatial scales (50 m - 500 m) were included (Henneberg et al. 2021, manuscript 1), compared to landscape composition at large spatial scales (300 m - 5000 m) (Henneberg et al. 2025; manuscript 2). When the influence of local tree hollow characteristics or forest structure at spatial scales of 50 m - 500 m around the focal tree hollows on threatened saproxylic beetle species richness was analyzed, pseudo-$R^2$ values that show the explanatory power of the models ranged from 0.288 to 0.691 in the Ebrach study region and from 0.203 to 0.487 in the Fichtelberg study region (Henneberg et al. 2021, manuscript 1). There were no significant effects of surrounding landscape composition on total species richness, therefore, these values could not be compared (see Henneberg et al. 2025; manuscript 2). In contrast, when the influence of the surrounding landscape composition at large spatial scales of 300 m - 5000 m on threatened saproxylic beetle species richness was analyzed, pseudo-$R^2$ values were smaller and ranged from 0.091 to 0.101 in the Ebrach study region and from 0.1 to 0.183 in the Fichtelberg study region (Henneberg et al. 2025; manuscript 2). Furthermore, the finding that total species richness of hollow-dwelling saproxylic beetles was not significantly related to large-scale landscape composition at any of the spatial scales of 300 m - 5000 m around the focal tree hollows in my study (Henneberg et al. 2025; manuscript 2) shows that at least this particular parameter of the surrounding landscape did not significantly affect the entirety of the saproxylic beetle community in the examined tree hollows. These results imply that, although landscape composition at large spatial scales of 300 m - 5000 m did significantly affect species richness of threatened saproxylic beetles in tree hollows, these effects were not as consistent and not as strong as the effects of local tree hollow characteristics and forest structure in the near surroundings of tree hollows and did not affect total species richness of saproxylic beetles.

**Non-beetle saproxylic taxa living in tree hollows (manuscript 3)**

Most studies on hollow-dwelling saproxylic insects have been conducted with beetles. Thus, in the third part of this study, we assessed the diversity of non-beetle saproxylic arthropods in tree hollows of the Ebrach forest region using DNA metabarcoding (Schauer, Henneberg et al. 2025; manuscript 3). We could show that Diptera was the most diverse order in the tree hollows we examined, contradicting the common doctrine in the literature where saproxylic beetles are regularly stated to be the most diverse taxon (Siitonen 2012). Our results support the assumption of Ulyshen (2018) who hypothesized that saproxylic Diptera might rival beetles as the most diverse insect order in dead wood. Compared to saproxylic beetles, saproxylic Diptera are less well-studied and species richness in different dead wood structures is often underestimated (Rotheray et al. 2001), which our results confirmed (Schauer, Henneberg et al. 2025; manuscript 3).

It has been stated that effects of parameters of tree hollows, hollow trees or forest structure on species richness of hollow-dwelling saproxylic species also depend on the examined species group (Schauer 2018; Müller et al. 2020). Our results regarding the diversity of non-beetle saproxylic species in tree hollows confirm that notion. For instance, species richness of hollow-dwelling Diptera in our study was negatively affected by the size of the hollow entrance (Schauer, Henneberg et al. 2025; manuscript 3), while saproxylic beetle species richness was positively affected (Henneberg et al. 2021, manuscript 1), which has been shown before in numerous studies (Ranius 2002; Ranius et al. 2009a, 2009b; Quinto et al. 2014, 2015; Schauer et al. 2018b). The preference of hollow-dwelling Diptera for a smaller entrance area can ecologically be explained by the fact that tree hollows with a smaller entrance area are associated with higher humidity inside the hollows and less evaporation (Ranius 2002; Micó 2018; Schauer et al. 2018b). Saproxylic Diptera usually represent the dominating species group in wet or saturated tree hollows (Hövemeyer & Schauermann 2003; Braccia & Batzer 2008; Ulyshen 2018), and many of these Diptera species are assumed to be obligate tree hollow colonizers (Blakely et al. 2012). It can be hypothesized that hollow-dwelling Diptera contain an even larger proportion of tree hollow specialists than saproxylic beetles as many larvae of Diptera are dependent on high humidity, and the relatively stable abiotic conditions within tree hollows (Siitonen 2012; Micó 2018) can permanently ensure a certain level of moisture suitable for larvae of hollow-dwelling Diptera.

Some effects, however, are similar for hollow-dwelling saproxylic beetles compared to other arthropod taxa in our study, namely the positive effect of a large hollow volume and the negative effect of degree of decomposition of the wood mold for species richness of hollow-dwelling Diptera, and the negative effect of height of the hollow entrance from ground for hollow-dwelling Hymenoptera (Schauer, Henneberg et al. 2025; manuscript 3). A positive effect of a large hollow volume on diversity of saproxylic Diptera in tree hollows has been shown before (Quinto et al. 2014; Sánchez-Galván et al. 2018). Hence, different hollow-dwelling taxa can benefit from the same characteristics of tree hollows. A large hollow volume, for instance, is positively associated with diversity of microhabitats within the hollow (habitat heterogeneity hypothesis, HHH). The HHH explains species diversity through heterogeneity of microhabitats that can support a great diversity of species with different habitat requirements (MacArthur & MacArthur 1961; Tews et al. 2004; Seibold et al. 2016). Furthermore, as species richness of hollow-dwelling saproxylic beetles can benefit from hollows being located close to the ground, and thus more accessible to species that crawl the forest floor (Ranius 2002; Schauer et al. 2018b), parasitoid hymenopterans might benefit from the greater diversity of potential host insects (Schauer, Henneberg et al. 2025; manuscript 3). Similarly, as early and intermediate stages of wood mold decomposition have been shown to benefit species richness of saproxylic beetles in tree hollows (Sverdrup-Thygeson et al. 2010; Schauer et al. 2018b; Henneberg et al. 2021, manuscript 1), the same effect was observed for hollow-dwelling Diptera (Schauer, Henneberg et al. 2025; manuscript 3). In this case, the ecological inference can be applied to different taxa of hollow-dwelling arthropods: the nutritional properties of highly decomposed wood mold do not support a broad community of arthropods anymore, which leads to a decline of species richness (Stokland & Siitonen 2012; Schauer et al. 2018b; Henneberg et al. 2021, manuscript 1).

The influence of certain parameters of tree hollows and forest structure on β-diversity of saproxylic arthropods in our study corroborate the notion that different hollow-dwelling saproxylic taxa have very distinct habitat requirements. Differences in tree circumference, size of the hollow entrance, amount of dead wood in a 100 m radius, or number of surrounding tree hollows in a 50 m radius around the focal tree hollows resulted in differing species composition of spiders (Araneae), springtails (Collembola), Diptera and Hymenoptera within the hollows (Schauer, Henneberg et al. 2025; manuscript 3). The finding that tree hollows with different characteristics in a given forest region may not just contain subsets of the species found in other hollows of the same tree species but a distinct assemblage of species implies that a high heterogeneity of tree hollows of different size and age, stage of decomposition, height above ground, etc. will help to increase overall diversity of arthropod communities in tree hollows (see Schauer et al. 2018). Furthermore, as high heterogeneity of tree hollows in a forest region will ensure high β-diversity in the hollows, i.e., high dissimilarity of species composition between hollows, it will prevent biotic homogenization and reduced ecosystem functionality in said forest region, and therefore increase resilience against disturbances (Olden et al. 2004; Gossner et al. 2016; Rolls et al. 2023). The insight that heterogeneity of tree hollows will benefit species richness of hollow-dwelling saproxylic beetles has been shown before (Seibold et al. 2016; Schauer 2018) but was shown here for the first time for hollow-dwelling Araneae, Collembola, Diptera and Hymenoptera (Schauer, Henneberg et al. 2025; manuscript 3).

## Implications for forest management

In this chapter I will make recommendations for forest management practitioners, political decision makers and conservationists that can be inferred from the results of this study. One of the most important results of this study is the insight that the influence of various parameters of tree hollows, forest structure or landscape structure on species richness within tree hollows varied substantially with regard to the surrounding environment or landscape. Thus, the surrounding environment or landscape should always be integrated to make informed decisions on management measures. In the Fichtelberg study region, for example, the most important parameter positively influencing species richness of hollow-dwelling saproxylic beetles was the proportion of beech trees at spatial scales up to 100 m around the focal tree hollows (Henneberg et al. 2021, manuscript 1). Therefore, in a forest region like Fichtelberg where the proportion of potentially suitable habitat for saproxylic species living in tree hollows of deciduous trees is very low, efforts should be made to increase the proportion of deciduous trees within a radius of 100 m to existing clusters of deciduous trees. In the Ebrach study region, in contrast, with a high proportion of deciduous trees the amount of dead wood up to a radius of 100 m around the focal tree hollows positively affected species richness of hollow-dwelling saproxylic beetles (Henneberg et al. 2021, manuscript 1). Hence, in forest regions with high proportions of deciduous trees the amount of dead wood of different types (standing or downed, different diameters, deciduous tree species and stages of decomposition) should be increased within a radius of 100 m to hollow-bearing trees to benefit hollow-dwelling arthropod communities.

Results of our landscape-scale study imply that threatened hollow-dwelling saproxylic beetles, i.e., the majority of tree hollow specialist beetle species, will benefit from conservation efforts at a landscape scale more than common species (Henneberg et al. 2025; manuscript 2). The proportion of potentially suitable habitat, i.e., the proportion of deciduous forest, surrounding the focal tree hollows positively affected species richness of threatened saproxylic beetles at spatial scales of up to 5000 m around the focal tree hollows in two of the three study regions (Henneberg et al. 2025; manuscript 2). Hence, conservation measures that aim at increasing the proportion of deciduous trees in managed forests will benefit those hollow-dwelling species that are most vulnerable and in need of effective conservation measures. Moreover, results of the study regions Fichtelberg and Kelheim, where patches of suitable habitat were affected by different types of isolation, imply that some species of saproxylic beetles might not readily disperse across open land. Therefore, a general increase in forest habitat connectivity, even coniferous forest, would greatly support the dispersal of hollow-dwelling saproxylic beetle species.

Results of our multi-taxon study (Schauer, Henneberg et al. 2025; manuscript 3) confirm the expectation that different hollow-dwelling species groups have distinct habitat requirements (Müller et al. 2020). Thus, high heterogeneity of tree hollows in a certain forest region will benefit the diversity of species assemblages in tree hollows (Seibold et al. 2016; Schauer 2018). Implications for forest management that can be derived include the conservation of all tree hollows and related microhabitat structures that might develop into tree hollows in the future (e.g., woodpecker holes, injuries of tree bark). Furthermore, prolonging the life of existing hollow trees is an important conservation measure to protect hollow-dwelling arthropod communities because among hollow trees the oldest and largest trees have a higher ecological value as they show a higher frequency of occurrence of tree hollows and hollow-related microhabitats (Ranius et al. 2009a; Siitonen 2012).

## Knowledge gaps - implications for future research

Many studies have been conducted on characteristics of tree hollows or hollow trees and their influence on species assemblages within the hollows (see Ranius 2002; Quinto et al. 2014; Taylor & Ranius 2014; Micó et al. 2015; Schauer et al. 2018b; Henneberg et al. 2021, manuscript 1; Schauer, Henneberg et al. 2025; manuscript 3). However, as most studies have been conducted on saproxylic beetles, there is an increased need for studies that focus on habitat requirements of other hollow-dwelling species groups. Furthermore, there are only few studies that do not only focus on characteristics of tree hollows or hollow trees but on resources in the surroundings of focal tree hollows (see Sverdrup-Thygeson et al. 2010; Schauer et al. 2018b; Henneberg et al. 2021, manuscript 1; Henneberg et al. 2025; manuscript 2), and these studies mostly focus on the amount of dead wood in the surroundings of tree hollows (see Müller et al. 2008; Sverdrup-Thygeson et al. 2010; Gossner et al. 2013; Müller et al. 2015a), the number of tree hollows in the surroundings (see Ranius et al. 2011; Musa et al. 2013; Pilskog et al. 2018) or the distance to potential dispersal sources (see Jansson et al.

2009; Kadej et al. 2016; Mestre et al. 2018). The question, which characteristics of the surrounding landscape at which spatial scales affect per-tree occurrence patterns and species richness of hollow-dwelling saproxylic arthropods remains an important study question for future studies. For example, many species of saproxylic beetles whose larvae develop in hollow trees visit flowers as adults (Wetherbee et al. 2020a; Ranius et al. 2024). But to my knowledge no studies have been conducted that examine the relationship between the abundance of flowers in the surroundings of tree hollows and occurrence patterns of saproxylic beetles in tree hollows.

Dispersal propensity of obligate tree hollow colonizers has been assumed to be rather low as they are specialized in stable and long-lasting habitats (Nilsson & Baranowski 1997; Travis & Dytham 1999; Hedin et al. 2008; Oleksa et al. 2013; Percel et al. 2019). However, except for a few well-studied species not much is known about the specific dispersal abilities of hollow-dwelling saproxylic insects, and in recent years some studies implied that the general notion of low dispersal ability among hollow-dwelling saproxylic arthropods cannot be maintained (see Feldhaar & Schauer 2018 for a review on the topic). Hence, more studies are needed on the dispersal ability of hollow-dwelling species and factors that might influence species' dispersal ability. For example, it has been shown that flight activity of the threatened hermit beetle, *Osmoderma eremita*, was positively influenced by temperature (Larsson & Svensson 2011), indicating stronger dispersal limitation in colder climates (Chiari et al. 2013).

Furthermore, a large gap in the study of saproxylic arthropod diversity within tree hollows occurs at a geographical level as arthropod assemblages in tree hollows have not been equally studied in all regions (Micó 2018). Although tree hollow density is high in tropical forests (Boyle et al. 2008; Vázquez & Renton 2015), arthropod assemblages in tree hollows have been poorly studied in tropical areas (Fincke 2009; Grove & Stork 1999; Seibold et al. 2015a; Micó 2018). The arthropod faunas in tree hollows have received more attention in Europe, in both temperate and Mediterranean forests where tree hollows, especially in old oak trees, have been widely studied (Micó 2018).

In my study conducted in three forest regions with differing forest structure and tree species composition I showed a varying influence of characteristics of tree hollows, hollow trees, forest structure and landscape composition on community composition of saproxylic arthropods, depending on the surrounding environment at different spatial scales (Henneberg et al. 2021, manuscript 1; Henneberg et al. 2025; manuscript 2). However, as most research on invertebrates in tree hollows represents a "snapshot" of one moment in time, it is necessary to conduct studies at a wider temporal scale to show the dynamics of species occurrence patterns and shifts in community composition over larger periods of time (Ranius et al. 2024). It has been shown that species turnover was high between tree hollows in the same forest region and even within the same tree hollow between years (Schauer et al. 2018b; Schauer, Henneberg et al. 2025; manuscript 3). Studies covering multiple years and regions that would integrate the changing climatic conditions and changes in land use (habitat amount and fragmentation) would be very beneficial from a conservation perspective as such studies could increase our understanding of how to address potential negative consequences of climate warming and habitat loss and fragmentation (Ranius et al. 2024).

This study provides important insights on scale dependency of hollow-dwelling saproxylic beetles in differently structured forest regions and habitat requirements of non-beetle arthropod taxa in tree hollows. However, there are still many knowledge gaps regarding the influence of the surrounding landscape at different spatial scales on hollow-dwelling arthropod communities. More studies on non-beetle arthropod taxa in tree hollows and the factors influencing them in different regions and at different spatial scales will further enhance our understanding of the complex interactions that shape the threatened tree hollow communities.

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# References

Alexander, K. N. A. (2002). The invertebrates of living and decaying timber in Britain and Ireland: a provisional annotated checklist. *English Nature Research Reports* No. 467.

Andersson, H. (1999). Red-listed or rare invertebrates associated with hollow, rotting or sapping trees or polypores in the town of Lund [in Swedish with an English summary]. *Entomologisk Tidskrift* **120:** 169-183.

Bauhus, J., Puettmann, K. & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management* **258:** 525-537.

Behan-Pelletier, V. & Walter, D. E. (2000). Biodiversity of oribatid mites (Acari: Oribatida) in tree canopies and litter. In: D. C. Coleman & P. F. Hendrix (Eds.) *Invertebrates as webmasters in ecosystems*. CABI Digital Library, pp. 187-202.

Berkov, A. (2018). Seasonality and stratification: neotropical saproxylic beetles respond to a heat and moisture continuum with conservatism and plasticity. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 547-578.

Blackman, M. W. & Stage, H. H. (1924). On the succession of insects living in the bark and wood of dying, dead and decaying hickory. Technical Publication No. 17. New York State College of Forestry: 3-269.

Blakely, T. J., Harding, J. S. & Didham, R. K. (2012). Distinctive aquatic assemblages in water-filled tree holes: a novel component of freshwater biodiversity in New Zealand temperate rainforests. *Insect Conservation and Diversity* **5:** 202-212.

Bowler, D. E. & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80:** 205-225.

Boyle, W. A., Ganong, C. N., Clark, D. B. & Hast, M. A. (2008). Density, distribution, and attributes of tree cavities in an old-growth tropical rain forest. *Biotropica* **40:** 241-245.

Braccia, A. & Batzer, D. P. (2008). Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats. *Canadian Journal of Forest Research* **38:** 2697-2704.

Buse, J., Ranius, T. & Assmann, T. (2008). An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conservation Biology* **22:** 329-337.

Cálix, M., Alexander, K. N., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalate, X., Aleksandrowicz, O., Audisio, P., Istrate, P., Jansson, N., Legakis, A., Liberto, A., Makris, C., Merkl, O., Pettersson, R. M., Schlaghamersky, J., Bologna, M. A., Brustel, H., Buse, J., Novák, V. & Purchart, L. (2018). European Red List of Saproxylic Beetles. IUCN, Brussels, 12 pp.

Carpaneto, G. M., Mazziotta, A. T., Coletti, G., Luiselli, L. M. & Audisio, P. A. (2010). Conflict between insect conservation and public safety: the case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *Journal of Insect Conservation* **14:** 555-565.

Casula, P., Fantini, S., Fenu, G., Fois, M., Calvia, G. & Bacchetta, G. (2021). Positive interactions between great longhorn beetles and forest structure. *Forest Ecology and Management* **486:** 118981.

Chiari, S., Carpaneto, G. M., Zauli, A., Marini, L., Audisio, P. & Ranius, T. (2012). Habitat of an endangered saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Ecoscience* **19:** 299-307.

Chiari, S., Carpaneto, G. M., Zauli, A., Zirpoli, G. M., Audisio, P. & Ranius, T. (2013). Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Insect Conservation and Diversity* **6:** 309-318.

Cockle, K. L., Martin, K. & Wesołowski, T. (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment* **9:** 377-382.

D'Angelo, S. A., Andrade, A. C. S., Laurance, S. G., Laurance, W. F. & Mesquita, R. C. G. (2004). Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology* **20:** 243-246.

Das, A. J., Stephenson, N. L. & Davis, K. P. (2016). Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* **97:** 2616-2627.

Drag, L., Hauck, D., Pokluda, P., Zimmermann, K. & Cizek, L. (2011). Demography and dispersal ability of a threatened saproxylic beetle: a mark-recapture study of the Rosalia Longicorn (*Rosalia alpina*). *PLoS One* **6:** e21345.

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E., Kadej, M., Kahlen, M., Köhler, F., Möller, G., Mühle, H., Sanchez, A., Schaffrath, U., Schmidl, J., Smolis, A., Szallies, A., Németh, T., Wurst, C., Thorn, S., Christensen, R. H. B. & Seibold, S. (2018). "Primeval forest relict beetles" of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *Journal of Insect Conservation* **22:** 15-28.

Elton, C. S. (1966). The pattern of animal communities. Methuen and Co. Ltd., London.

Feldhaar, H. & Schauer, B. (2018). Dispersal of saproxylic insects. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 515-546.

Fierro, A., Vergara, P. M., Carvajal, M. A., Zúñiga, A. H. & Alaniz, A. J. (2024). Understanding how habitat conditions modulate the impact of ecosystem engineers on tree-hollow-dwelling organisms. *Ecological Engineering* **201:** 107207.

Fincke, O. M. (1999). Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority. *Ecological Entomology* **24:** 13-23.

Floren, A. & Schmidl, J. (2008). Introduction: Canopy arthropod research in Europe. In: A. Floren, J. Schmidl (Eds.) *Canopy arthropod research in Europe*. Bioform Entomology, Nürnberg, pp. 13-20.

Floren, A., Müller, T., Dittrich, M., Weiss, M. & Linsenmair, K. E. (2014). The influence of tree species, stratum and forest management on beetle assemblages responding to deadwood enrichment. *Forest Ecology and Management* **323:** 57-64.

Franc, N., Götmark, F., Økland, B., Nordén, B., & Paltto, H. (2007). Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation* **135:** 86-98.

García-López, A., Galante, E. & Micó, E. (2016). Saproxylic beetle assemblage selection as determining factor of species distributional patterns: implications for conservation. *Journal of Insect Science* **16:** 45.

Gibbons, P. & Lindenmayer, D. (2002). Tree hollows and wildlife conservation in Australia. Csiro publishing, 240 pp.

Gibbons, P., Lindenmayer, D. B., Fischer, J., Manning, A. D., Weinberg, A., Seddon, J., Ryan, P. & Barrett, G. (2008). The future of scattered trees in agricultural landscapes. *Conservation Biology* **22:** 1309-1319.

Gimmel, M. L. & Ferro, M. L. (2018). General overview of saproxylic Coleoptera. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 51-128.

Gonzalez-Akre, E., Meakem, V., Eng, C.-Y., Tepley, A. J., Bourg, N. A., McShea, W., Davies, S. J. & Anderson-Teixeira, K. (2016). Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. *Ecography* **7:** Article e01595.

Gossner, M. M., Floren, A., Weisser, W. W. & Linsenmair, K. E. (2013). Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. *Forest Ecology and Management* **302:** 404-413.

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S. C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Ré Jorge, L., Jung, K., Keyel, A. C., Klein, A.-M., Klemmer, S., Krauss, J., Lange, M., … & Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* **540:** 266-269.

Gossner, M. M. & Müller, J. (2011). The influence of species traits and q-metrics on scale-specific β-diversity components of arthropod communities of temperate forests. *Landscape Ecology* **26:** 411-424.

Götmark, F., Åsegård, E. & Franc, N. (2011). How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. *Forest Ecology and Management* **262:** 2297-2305.

Gouix, N. & Brustel, H. (2012). Emergence trap, a new method to survey *Limoniscus violaceus* (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation* **21:** 421-436.

Gouix, N., Sebek, P., Valladares, L., Brustel, H., & Brin, A. (2015). Habitat requirements of the violet click beetle (*Limoniscus violaceus*), an endangered umbrella species of basal hollow trees. *Insect Conservation and Diversity* **8:** 418-427.

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* **33:** 1-23.

Grove, S. J. & Stork, N. E. (1999). The conservation of saproxylic insects in tropical forests: a research agenda. *Journal of Insect Conservation* **3:** 67-74.

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Kiebacher, T., Kormann, U. G., Scheidegger, C., Schmidt, R., Stillhard, J., Szallies, A., Pellissier, L. & Lachat, T. (2021). Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. *Landscape Ecology* **36:** 89-104.

Hammond, H. E. J., Langor, D. W. & Spence, J. R. (2001). Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). *Canadian Journal of Forest Research* **31:** 1175-1183.

Hammond, H. J., Langor, D. W. & Spence, J. R. (2017). Changes in saproxylic beetle (Insecta: Coleoptera) assemblages following wildfire and harvest in boreal *Populus* forests. *Forest Ecology and Management* **401:** 319-329.

Hanski, I. & Hammond, P. M. (1995). Biodiversity in boreal forests. *Trends in Ecology and Evolution* **10:** 5-6.

Hanski, I., Kuussaari, M. & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* **75:** 747-762.

Hartel, T., Dorresteijn, I., Klein, C., Máthé, O., Moga, C. I., Öllerer, K., Roellig, M., von Wehrden, H. & Fischer, J. (2013). Wood-pastures in a traditional rural region of Eastern Europe: Characteristics, management and status. *Biological Conservation* **166:** 267-275.

Hedin, J., Ranius, T., Nilsson, S. G. & Smith, H. G. (2008). Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity and Conservation* **17:** 675-684.

Henneberg, B., Bauer, S., Birkenbach, M., Mertl, V., Steinbauer, M. J., Feldhaar, H. & Obermaier, E. (2021). Influence of tree hollow characteristics and forest structure on saproxylic beetle diversity in tree hollows in managed forests in a regional comparison. *Ecology and Evolution* **11:** 17973-17999.

Henneberg, B., Feldhaar, H., Förtsch, S., Schauer, B. & Obermaier, E. (2024). Threatened saproxylic beetle species in tree hollows react more sensitively to surrounding landscape composition in central European managed forests than total species richness. *Biodiversity and Conservation*, in revision.

Hövemeyer, K. & Schauermann, J. (2003). Succession of Diptera on dead beech wood: a 10-year study. *Pedobiologia* **47:** 61-75.

Jacobsen, R. M., Sverdrup-Thygeson, A. & Birkemoe, T. (2015). Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. *Journal of Insect Conservation* **19:** 1053-1062.

Jansson, N., Ranius, T., Larsson, A. & Milberg, P. (2009). Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and Conservation* **18:** 3891-3908.

Jonsell, M., Nordlander, G. & Jonsson, M. (1999). Colonization patterns of insects breeding in wood-decaying fungi. *Journal of Insect Conservation* **3:** 145-161.

Jonsson, M. (2003). Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *Ecological Entomology* **28:** 159-167.

Jonsson, M., Johannesen, J. & Seitz, A. (2003). Comparative genetic structure of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *Journal of Insect Conservation* **7:** 111-124.

Jonsson, B. G. (2012). Population dynamics and evolutionary strategies. In: J. N. Stokland, J. Siitonen, B. G. Jonsson (Eds.) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 338-355.

Jönsson, N., Méndez, M. & Ranius, T. (2004). Nutrient richness of wood mould in tree hollows with the Scarabaeid beetle *Osmoderma eremita*. *Animal Biodiversity and Conservation* **27:** 79-82.

Kadej, M., Zając, K., Smolis, A., Tarnawski, D. & Malkiewicz, A. (2016). Isolation from forest habitats reduces chances of the presence of *Osmoderma eremita* sensu lato (Coleoptera: Scarabaeidae) in rural avenues. *Journal of Insect Conservation* **20:** 395-406.

Khazan, E. S., Bright, E. G. & Beyer, J. E. (2015). Land management impacts on tree hole invertebrate communities in a neotropical rainforest. *Journal of Insect Conservation* **19:** 681-690.

Kletečka, Z. (1996). The xylophagus beetles (Insecta, Coleoptera) community and its succession on Scotch elm (*Ulmus glabra*) branches. *Biológia (Bratislava)* **51:** 143-152.

Koch Widerberg, M., Ranius, T., Drobyshev, I., Nilsson, U. & Lindbladh, M. (2012). Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodiversity and Conservation* **21:** 3035-3059.

Köhler, F. (2000). Totholzkäfer in Naturwaldzellen des nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung. [Saproxylic Beetles in Nature Forests of the Northern Rhineland. Comparative Studies on the Saproxylic Beetles of Germany and Contributions to German Nature Forest Research]. Recklinghausen: Landesamt Agrarordnung NRW. 351 pp.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A. & Winter, S. (2016). Catalogue of tree microhabitats: Reference field list. *Integrate+ Technical Paper.* 16pp.

Larsson, M. C. & Svensson, G. P. (2011). Monitoring spatiotemporal variation in abundance and dispersal by a pheromone-kairomone system in the threatened saproxylic beetles *Osmoderma eremita* and *Elater ferrugineus*. *Journal of Insect Conservation* **15:** 891-902.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* **11:** 1027-1039.

Lindenmayer, D., Hobbs, R. J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., … & Zavaleta, E. (2008). A checklist for ecological management of landscapes for conservation. *Ecology Letters* **11:** 78-91.

Lindenmayer, D. B., Laurance, W. F. & Franklin, J. F. (2012). Global decline in large old trees. *Science* **338:** 1305-1306.

Lindhe, A., Lindelöw, Å. & Åsenblad, N. (2005). Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation* **14:** 3033-3053.

Lindman, L., Öckinger, E. & Ranius, T. (2023). Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*. *Ecological Entomology* **48:** 112-126.

Maass, J. M., Martínez-Yrízar, A., Patino, C. & Sarukhán, J. (2002). Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem. *Journal of Tropical Ecology* **18:** 821-834.

MacArthur, R. H. & MacArthur, J. W. (1961). On bird species diversity. *Ecology* **42:** 594-598.

Manning, A. D., Fischer, J. & Lindenmayer, D. B. (2006). Scattered trees are keystone structures–implications for conservation. *Biological Conservation* **132:** 311-321.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation* **94:** 199-209.

Martin, M. M. (1991). The evolution of cellulose digestion in insects. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **333:** 281-288.

Martínez-Devesa, G., Hernández-Corral, J. & Micó, E. (2024). Spatio-temporal species aggregations do not rule out interspecific competition in tree hollow spider assemblages. *Ecological Entomology* **49:** 106-118.

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., Turner, M. G., Uriarte, M., Walker, A. P. & Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science* **368:** eaaz9463.

Mestre, L., Jansson, N. & Ranius, T. (2018). Saproxylic biodiversity and decomposition rate decrease with small-scale isolation of tree hollows. *Biological Conservation* **227:** 226-232.

Micó, E. (2018). Saproxylic insects in tree hollows. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 693-727.

Micó, E., García-Lòpez, A., Brustel, H., Padilla, A. & Galante, E. (2013). Explaining the saproxylic beetle diversity of a protected Mediterranean area. *Biodiversity and Conservation* **22:** 889-904.

Micó, E., García-López, A., Sánchez, A., Juárez, M. & Galante, E. (2015). What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? *Journal of Insect Conservation* **19:** 141-153.

Milberg, P., Bergman, K. O., Johansson, H. & Jansson, N. (2014). Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. *Insect Conservation and Diversity* **7:** 508-522.

Mitrus, S., Hebda, G. & Wesołowski, T. (2016). Cohabitation of tree holes by ants and breeding birds in a temperate deciduous forest. *Scandinavian Journal of Forest Research* **31:** 135-139.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M. M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L. & Gossner, M. M. (2015a). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography* **38:** 499-509.

Müller, J., Bußler, H., Bense, U., Brustel, H. & Flechtner, G. (2005). Urwald relict species–Saproxylic beetles indicating structural qualities and habitat tradition. *Waldökologie online: AFSV-Berichte der Arbeitsgemeinschaft Forstliche Standorts- und Vegetationskunde* **2:** 106-113.

Müller, J., Bußler, H. & Kneib, T. (2008). Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation* **12:** 107-124.

Müller, J. & Gossner, M. M. (2010). Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biological Conservation* **143:** 625-633.

Müller, J., Jarzabek-Müller, A., Bußler, H. & Gossner, M. M. (2014b). Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation* **17:** 154-162.

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V. & Thorn, S. (2020). Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos* **129:** 1579-1588.

Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K. E., Weisser, W. W. & Gossner, M. M. (2015b). Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *Journal of Applied Ecology* **52:** 753-762.

Musa, N., Andersson, K., Burman, J., Andersson, F., Hedenström, E., Jansson, N., Paltto, H., Westerberg, L., Winde, I., Larsson, M. C., Bergman, K.-O. & Milberg, P. (2013). Using sex pheromone and a multi-scale approach to predict the distribution of a rare saproxylic beetle. *PLoS One* **8:** e66149.

Nilssen, A. C. (1984). Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. *Annales Entomologici Fennici* **50:** 37–42.

Nilsson, T. (1997). Spatial population dynamics of the black tinder fungus beetle, *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae). Doctoral dissertation, Acta Universitatis Upsaliensis, Sweden.

Nilsson, S. G. & Baranowski, R. (1997). Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* **20:** 491-498.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity & Conservation* **5:** 75-100.

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* **19:** 18-24.

Oleksa, A., Chybicki, I. J., Gawroński, R., Svensson, G. P. & Burczyk, J. (2013). Isolation by distance in saproxylic beetles may increase with niche specialization. *Journal of Insect Conservation* **17:** 219-233.

Oleksa, A., Chybicki, I. J., Larsson, M. C., Svensson, G. P., & Gawroński, R. (2015). Rural avenues as dispersal corridors for the vulnerable saproxylic beetle *Elater ferrugineus* in a fragmented agricultural landscape. *Journal of Insect Conservation* **19:** 567-580.

Oleksa, A. & Gawroński, R. (2006). Forest insects in an agricultural landscape—presence of old trees is more important than the existence of nearby forest. *Ecological Questions* **7:** 29-36.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastiá, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology* **24:** 101-112.

Park, O. & Auerbach, S. (1954). Further study of the tree-hole complex with emphasis on quantitative aspects of the fauna. *Ecology* **35:** 208-222.

Percel, G., Laroche, F. & Bouget, C. (2019). The scale of saproxylic beetles response to landscape structure depends on their habitat stability. *Landscape Ecology* **34:** 1905-1918.

Pilskog, H. E., Sverdrup-Thygeson, A., Evju, M., Framstad, E. & Birkemoe, T. (2018). Long-lasting effects of logging on beetles in hollow oaks. *Ecology and Evolution* **8:** 10126-10137.

Quinto, J., Marcos-García, M. D. L. Á., Diaz-Castelazo, C., Rico-Gray, V., Galante, E. & Micó, E. (2015). Association patterns in saproxylic insect networks in three Iberian Mediterranean woodlands and their resistance to microhabitat loss. *PLoS One* **10:** e0122141.

Quinto, J., Micó, E., Martínez-Falcón, A. P., Galante, E. & Marcos-García, M. D. L. Á. (2014). Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *Journal of Insect Conservation* **18:** 981-992.

Ranius, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation* **103:** 85-91.

Ranius, T., Gibbons, P. & Lindenmayer, D. (2024). Habitat requirements of deadwood-dependent invertebrates that occupy tree hollows. *Biological Reviews,* doi: 10.1111/brv.13110.

Ranius, T. & Hedin, J. (2001). The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* **126:** 363-370.

Ranius, T. & Jansson, N. (2000). The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* **95:** 85-94.

Ranius, T., Johansson, V. & Fahrig, L. (2011). Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. *Biodiversity and Conservation* **20:** 2027-2040.

Ranius, T., Johansson, V., Schroeder, M. & Caruso, A. (2015). Relative importance of habitat characteristics at multiple spatial scales for wood-dependent beetles in boreal forest. *Landscape Ecology* **30:** 1931-1942.

Ranius, T., Niklasson, M. & Berg, N. (2009a). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management* **257:** 303-310.

Ranius, T. & Nilsson, S. G. (1997). Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *Journal of Insect Conservation* **1:** 193-204.

Ranius, T., Svensson, G. P., Berg, N., Niklasson, M. & Larsson, M. C. (2009b). The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Annales Zoologici Fennici* **46:** 205-216.

Ranius, T. & Wilander, P. (2000). Occurrence of *Larca lata* H. J. Hansen (Pseudoscorpionida: Garypidae) and *Allochernes wideri* C. L. Koch (Pseudoscorpionida: Chernetidae) in tree hollows in relation to habitat quality and density. *Journal of Insect Conservation* **4:** 23-31.

Remm, J. & Lõhmus, A. (2011). Tree cavities in forests–the broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management* **262:** 579-585.

Rolls, R. J., Deane, D. C., Johnson, S. E., Heino, J., Anderson, M. J. & Ellingsen, K. E. (2023). Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews* **98:** 1388-1423.

Rotheray, G. E., Hancock, G., Hewitt, S., Horsfield, D., MacGowan, I., Robertson, D. & Watt, K. (2001). The biodiversity and conservation of saproxylic Diptera in Scotland. *Journal of Insect Conservation* **5:** 77-85.

Sánchez, A., Micó, E., Galante, E. & Juárez, M. (2017). Chemical transformation of Quercus wood by Cetonia larvae (Coleoptera: Cetoniidae): an improvement of carbon and nitrogen available in saproxylic environments. *European Journal of Soil Biology* **78:** 57-65.

Sánchez-Galván, I. R., Marcos-García, M. Á., Galante, E., Azeria, E. T. & Micó, E. (2018). Unraveling saproxylic insect interactions in tree hollows from Iberian Mediterranean Forest. *Environmental Entomology* **47:** 300-308.

Schauer, B. (2018). *Saproxylic insects in tree hollows: drivers of diversity, dispersal and food web structure*. Doctoral dissertation, University of Bayreuth, 225 pp.

Schauer, B., Bong, J., Popp, C., Obermaier, E. & Feldhaar, H. (2018a). Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. *Basic and Applied Ecology* **32:** 26-38.

Schauer, B., Henneberg, B., Obermaier, E. & Feldhaar, H. (2024). Tree hollow parameters and their effects on saproxylic arthropod diversity: a multi-taxon approach. *Insect Conservation and Diversity*, submitted.

Schauer, B., Steinbauer, M. J., Vailshery, L. S., Müller, J., Feldhaar, H. & Obermaier, E. (2018b). Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation* **27:** 853-869.

Schmidl, J. & Büche, B. (2018). Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick. Naturschutz und Biologische Vielfalt **70** (in press).

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D. & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology* **53:** 934-943.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S. & Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology* **98:** 1613-1622.

Seibold, S., Bässler, C., Brandl, R., Gossner, M. M., Thorn, S., Ulyshen, M. D. & Müller, J. (2015a). Experimental studies of dead-wood biodiversity—a review identifying global gaps in knowledge. *Biological Conservation* **191:** 139-149.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2015b). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology* **29:** 382-390.

Seibold, S. & Thorn, S. (2018). The importance of dead-wood amount for saproxylic insects and how it interacts with dead-wood diversity and other habitat factors. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 607-637.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* **49:** 11-42.

Siitonen, J. (2012). Microhabitats. In: J. N. Stokland, J. Siitonen, B. G. Jonsson (Eds.) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 150-182.

Sirami, C., Jay-Robert, P., Brustel, H., Valladares, L., Le Guilloux, S. & Martin, J. L. (2008). Saproxylic beetle assemblages of old Holm-oak trees in the Mediterranean region: role of a keystone structure in a changing heterogeneous landscape. *Revue d'Écologie* **63:** 101-114.

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg. 79 pp.

Srivastava, D. S. & Lawton, J. H. (1998). Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist* **152:** 510-529.

Stubbs, A. E. (1972). Wildlife conservation and dead wood. A supplement to the Journal of Devon Trust for Nature Conservation. 18 pp.

Stokland, J. N. (2012). Wood decomposition. In: J. N. Stokland, J. Siitonen, B. G. Jonsson (Eds.) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 10-28.

Stokland, J. N. & Siitonen, J. (2012). Mortality factors and decay succession. In: J. N. Stokland, J. Siitonen, B. G. Jonsson (Eds.) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 110-149.

Stokland, J. N., Siitonen, J. & Jonsson, B. G. (2012). Introduction. In: J. N. Stokland, J. Siitonen, B. G. Jonsson (Eds.) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 1-9.

Svensson, M., Dahlberg, A., Ranius, T. & Thor, G. (2014). Dead branches on living trees constitute a large part of the dead wood in managed boreal forests, but are not important for wood-dependent lichens. *Journal of Vegetation Science* **25:** 819-828.

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014). Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and Conservation* **23:** 513-535.

Sverdrup-Thygeson, A., Skarpaas, O. & Ødegaard, F. (2010). Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation* **19:** 837-852.

Sverdrup-Thygeson, A., Skarpaas, O., Blumentrath, S., Birkemoe, T. & Evju, M. (2017). Habitat connectivity affects specialist species richness more than generalists in veteran trees. *Forest Ecology and Management* **403:** 96-102.

Swift, T. L. & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews* **85:** 35-53.

Taylor, A. R. & Ranius, T. (2014). Tree hollows harbour a specialised oribatid mite fauna. *Journal of Insect Conservation* **18:** 39-55.

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

Thomas, C. D. (2000). Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267:** 139-145.

Travis, J. M. & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266:** 723-728.

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. & Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological Reviews* **87:** 661-685.

Ulyshen, M. D. (2018). Saproxylic Diptera. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 167-192.

Ulyshen, M. D., & Šobotník, J. (2018). An introduction to the diversity, ecology, and conservation of saproxylic insects. In: M. D. Ulyshen (Ed.) *Saproxylic insects: diversity, ecology and conservation. Zoological Monographs, Vol. 1.* Springer, Cham, pp. 1-47.

Vázquez, L. & Renton, K. (2015). High density of tree-cavities and snags in tropical dry forest of western Mexico raises questions for a latitudinal gradient. *PLoS One* **10:** e0116745.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2021). Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. *Insect Conservation and Diversity* **14:** 132-143.

Wetherbee, R., Birkemoe, T., Asplund, J., Renčo, M. & Sverdrup-Thygeson, A. (2022). It takes a community to maintain a tree hollow: Food web complexity enhances decomposition and wood mould production. *Functional Ecology* **36:** 2215-2226.

Wetherbee, R., Birkemoe, T., Skarpaas, O. & Sverdrup-Thygeson, A. (2020a). Hollow oaks and beetle functional diversity: Significance of surroundings extends beyond taxonomy. *Ecology and Evolution* **10:** 819-831.

Wetherbee, R., Birkemoe, T. & Sverdrup-Thygeson, A. (2020b). Veteran trees are a source of natural enemies. *Scientific Reports* **10:** 18485.

Zahner, V., Sikora, L. & Pasinelli, G. (2012). Heart rot as a key factor for cavity tree selection in the black woodpecker. *Forest Ecology and Management* **271:** 98-103.

# Appendix

**Publication LWF aktuell:**

## Artenvielfalt in Mulmhöhlen: Einfluss von Waldstruktur und Höhleneigenschaften (2022)

Benjamin Henneberg, Heike Feldhaar, Elisabeth Obermaier

# Artenvielfalt in Mulmhöhlen: Einfluss von Waldstruktur und Höhleneigenschaften

**Benjamin Henneberg, Heike Feldhaar, Elisabeth Obermaier**

**Spätestens seitdem der Bayerische Ministerrat im Jahr 2008 die Strategie zum Erhalt der biologischen Vielfalt in Bayern – kurz: Bayerische Biodiversitätsstrategie – beschlossen hat, steht neben der Sicherung der Artenvielfalt auch der Erhalt der Lebensraumvielfalt auf der Agenda.**

1 Der Schnellkäfer *Melanotus rufipes* ist eine xylobionte Käferart, die im Rahmen der Studie in allen drei untersuchten Waldgebieten gefunden wurde. Foto: Andreas Haselböck, www.naturspaziergang.de

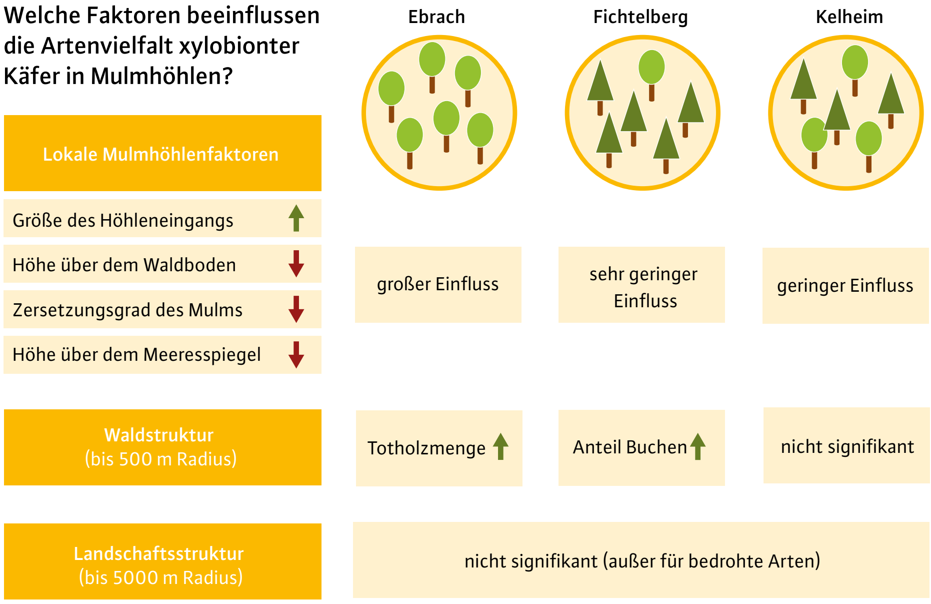
Ein wichtiger Lebensraumtyp für die Artenvielfalt in Wäldern sind sogenannte Mulmhöhlen – Faulhöhlen in lebenden Bäumen, die sich in der Regel in alten Laubbäumen entwickeln (Nadelbäume erschweren aufgrund des starken Harzflusses die Bildung von Höhlen). Mulmhöhlen bilden sich vor allem in höherem Baumalter, ihre Entwicklung dauert viele Jahre. Bei Eichen zum Beispiel nimmt die Wahrscheinlichkeit der Höhlenbildung ab einem Alter von etwa 200 Jahren stark zu (Ranius et al. 2009).

## Xylobionte Mulmhöhlenbewohner – der Wohnraum ist knapp

Tiere, die in mindestens einer Phase ihres Lebens direkt oder indirekt auf Totholz angewiesen sind, werden als xylobiont bezeichnet (Speight 1989). Schätzungsweise 34 % aller in mitteleuropäischen Wäldern vorkommenden Arten gelten als xylobiont (Müller et al. 2008), bei den Käfern sogar über 50 % (Grove 2002). Xylobionte Arten machen somit einen großen Teil der Artenvielfalt im Wald aus. Sie sind darüber hinaus wichtig für den Nährstoffkreislauf im Wald, da sie maßgeblich an der Zersetzung von Totholz beteiligt sind.

Mulmhöhlen bieten Lebensraum für zahlreiche Tiergruppen. Die größte Gruppe bilden die Gliederfüßer (Arthropoden), hiervon vor allem Fliegen und Mücken (Dipteren), Käfer (Coleopteren), aber auch Milben (Acari) und Springschwänze (Collembola). Mulmhöhlen sind außerdem ein Habitat für höhlenbrütende Vögel und Säugetiere, wie z. B. Fledermäuse. Folglich stellen Mulmhöhlen Schlüsselstrukturen für eine hohe Artenvielfalt im Wald dar (Müller et al. 2014). Da alte Höhlenbäume aufgrund des geringen wirtschaftlichen Werts in der Vergangenheit häufig entfernt wurden, zählen Mulmhöhlen heute zu den seltensten Strukturen in mitteleuropäischen Wäldern (Lindenmayer et al. 2012). Diese Lebensraumknappheit hat zur Folge, dass vor allem die Mulmhöhlenspezialisten unter den Käfern, also Arten, die nur in Mulmhöhlen ihre Larvalentwicklung vollziehen können, zu den gefährdetsten Tiergruppen gehören. Etwa 75 % von ihnen stehen auf der Roten Liste (Schmidl & Büche 2018).

So vielfältig wie ihre Bewohner sind Mulmhöhlen auch in Bezug auf ihre Eigenschaften (Micó et al. 2015; Schauer et al. 2018). Es gibt große und kleine Mulmhöhlen, Höhlen mit großflächigem oder kleinem Eingang, feuchte und weniger feuchte Höhlen, Höhlen mit grobem, wenig zersetztem Mulm oder solche mit dunklem, stark zersetztem Mulm. Auch die Habitatansprüche der Mulmhöhlenbewohner sind sehr unterschiedlich. Manche Arten besiedeln nur sehr feuchte Höhlen, andere nur tiefgelegene Höhlen mit Kontakt zum Waldboden oder ausschließlich große Höhlen. Diese besonderen Ansprüche vieler Arten verringern das Angebot an passenden Mulmhöhlen zusätzlich.

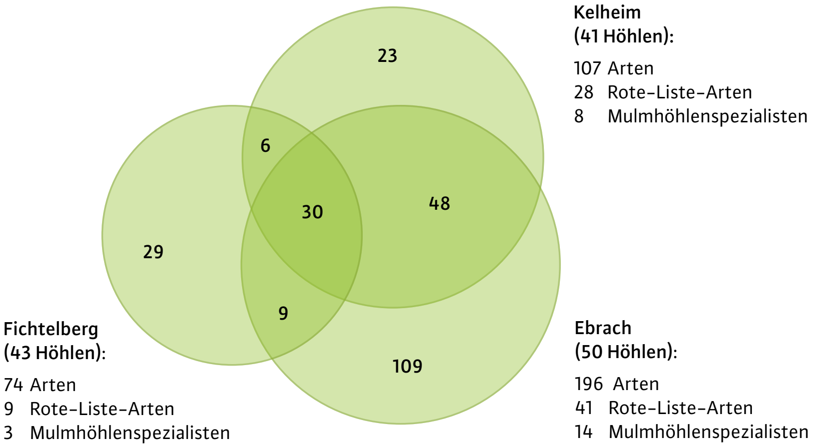


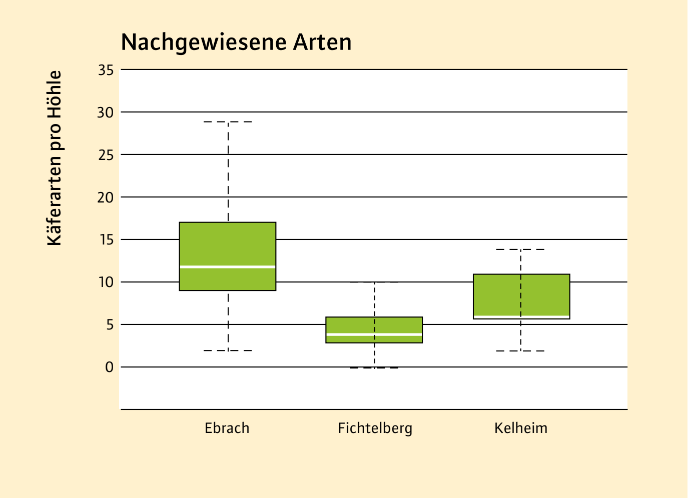
**Welche Faktoren beeinflussen die Artenvielfalt xylobionter Käfer in Mulmhöhlen?**

| | Ebrach | Fichtelberg | Kelheim |
|---|---|---|---|
| Lokale Mulmhöhlenfaktoren<br>Größe des Höhleneingangs ↑<br>Höhe über dem Waldboden ↓<br>Zersetzungsgrad des Mulms ↓<br>Höhe über dem Meeresspiegel ↓ | großer Einfluss | sehr geringer Einfluss | geringer Einfluss |
| Waldstruktur (bis 500 m Radius) | Totholzmenge ↑ | Anteil Buchen ↑ | nicht signifikant |
| Landschaftsstruktur (bis 5000 m Radius) | nicht signifikant (außer für bedrohte Arten) | | |

2 Umweltfaktoren, die die Artenvielfalt xylobionter Käfer in den untersuchten Mulmhöhlen beeinflussen. Grüner Pfeil = positiver Einfluss (z. B. je größer der Höhleneingang, desto höher die Artenvielfalt), roter Pfeil = negativer Einfluss (z. B. je höher der Zersetzungsgrad des Mulms, desto geringer die Artenvielfalt). Die jeweilige Baumartenzusammensetzung der drei Waldgebiete wird durch das Verhältnis von Laub- und Nadelbäumen in den Kreisen visualisiert.

**3** Mulmhöhle in einer Rotbuche im Forstbetrieb Ebrach. Höhleneingang etwa 80 cm über dem Waldboden. Foto: B. Henneberg, Universität Bayreuth





**4** Artenvielfalt xylobionter Käfer in den untersuchten Mulmhöhlen der drei Waldgebiete. Arten, die in zwei oder mehr Waldgebieten nachgewiesen wurden, werden durch die Schnittmengen dargestellt (oben). Boxplots visualisieren die Anzahl xylobionter Käferarten pro Höhle, die in den drei Waldgebieten nachgewiesen wurden (unten).

## Forstliche Forschung: Vergleich dreier Waldgebiete

Aus dem Projekt *Nahrungsbeziehungen und Ausbreitungsdistanzen von Mulmhöhlenarthropoden* ergaben sich bereits Erkenntnisse über Mulmhöhlen-Artengemeinschaften in einem bewirtschafteten Laubwald und deren lokale Habitatansprüche (Schauer et al., LWF aktuell 3/2018). Die hier vorgestellte Studie im Folgeprojekt *Arthropodengemeinschaften in Mulmhöhlen im Landschaftskontext: Einfluss der Wald- und der Landschaftsstruktur auf Diversität und Ausbreitungsdistanzen im regionalen Vergleich«* wurde auf insgesamt drei Betriebe der Bayerischen Staatsforsten (BaySF) mit unterschiedlicher Baumartenzusammensetzung ausgeweitet (Henneberg et al. 2021). Zielsetzung der Studie war es, auf größeren räumlichen Skalen die Auswirkungen der Landschafts- und Waldstruktur (z. B. Totholzmenge, Baumartenzusammensetzung, Altersstruktur) auf die Artenvielfalt von Arthropoden in Mulmhöhlen sowie deren Ausbreitungsdistanzen mit Hilfe von regelmäßig erhobenen BaySF-Forstinventur- und Fernerkundungsdaten zu untersuchen. Darüber hinaus wurden Erkenntnisse aus bisherigen Studien, die sich vor allem mit lokalen Faktoren der Mulmhöhlen und Höhlenbäume beschäftigten, in drei Waldgebieten validiert.

Neben dem Forstbetrieb Ebrach, der sich durch Eichen- und Buchenbestände auszeichnet, wurde der Forstbetrieb Kelheim untersucht, der gemischte Laub- und Nadelwälder aufweist, sowie der Forstbetrieb Fichtelberg, der durch montane, fast reine Fichtenbestände mit gelegentlichen Laubbaumvorkommen charakterisiert ist (Abbildung 2). In jedem der drei Waldgebiete wurden in den Jahren 2018 und 2019 jeweils einmal 40 bis 50 Mulmhöhlen in Rotbuchen mit Emergenzfallen beprobt. Dabei wurden die von April bis September aus den Mulmhöhlen entweichenden Insekten gefangen und in Alkohol konserviert. Dieses Verfahren hat den Vorteil, dass es nicht invasiv ist und die wertvollen Mulmhöhlen sowie der darin befindliche Mulm intakt bleiben (Schauer et al. 2018). Die Larvalentwicklung von mulmhöhlenbewohnenden Käfern erstreckt sich in der Regel über mehrere Jahre – folglich sind Larven, die im Jahr der Beprobung ihre Entwicklung noch nicht vollendet hatten, in den Höhlen verblieben und können in den Folgejahren schlüpfen.

## Lokale Eigenschaften der Mulmhöhlen von großer Bedeutung

In den 134 beprobten Mulmhöhlen der drei Untersuchungsgebiete wurden insgesamt 283 xylobionte Käferarten aus 48 Familien gesammelt (5.880 Individuen). Davon stehen 62 Arten auf der Roten Liste, was einem Anteil bedrohter Arten von 22 % entspricht. 16 Arten wurden als Mulmhöhlenspezialisten identifiziert, die alle auf der Roten Liste stehen. Die Anzahl nachgewiesener Arten sowie die Zusammensetzung der Artengemeinschaften unterschied sich teilweise deutlich zwischen den drei untersuchten Waldgebieten (Abbildung 4). Mulmhöhlen im Forstbetrieb Ebrach wiesen die größte Artenvielfalt pro Höhle auf (im Durchschnitt 13,2 Käferarten pro Höhle, Fichtelberg: 4,6, Kelheim: 7,9), wie auch die höchste Anzahl gefährdeter Arten und Mulmhöhlenspezialisten. Es zeigte sich, dass die Artenvielfalt besonders von den lokalen Eigenschaften der Mulmhöhlen selbst sowie der Höhlenbäume beeinflusst wurde (Abbildung 2). So fanden sich z. B. mehr Käferarten in Mulmhöh-

**5** Fangbereite Emergenzfalle an einer Rotbuche im Forstbetrieb Ebrach. Der einzige Weg für mulmhöhlenbewohnende Insekten aus der mit schwarzem Stoff verschlossenen Höhle führt durch einen Kunststoffschlauch in den mit Ethanol gefüllten Probenbehälter. Dort werden die Insekten für die Wissenschaft konserviert. Stahlstangen, Kabelbinder, Holzklötze und ein Spanngurt halten den Probenbehälter in Position, wenn der Höhleneingang sich nicht in Bodennähe befindet.
Foto: B. Henneberg, Universität Bayreuth

len mit großflächigen Höhleneingängen und in bodennahen Höhlen. Weiterhin waren in Höhlen mit noch gering zersetztem und dementsprechend hellerem und grobkörnigerem Mulm mehr Käferarten als in Höhlen mit bereits stärker zersetztem Mulm. Der noch frische Mulm kann wahrscheinlich von einer größeren Zahl auch generalistischer xylobionter Arten genutzt werden, während den stark zersetzten, dunklen Mulm vorwiegend wenige Spezialisten dieser Zersetzungsstadien annehmen (Gouix et al. 2015).

### Bedeutung der Waldstruktur

Die Artenvielfalt in den Mulmhöhlen wurde vor allem im Hinblick auf den Einfluss der Waldstruktur im Umkreis von bis zu 500 m um die Mulmhöhlen untersucht. Zu diesem Zweck konnten wir die regelmäßig erhobenen Forstinventurdaten der BaySF nutzen, die über ein Raster an Inventurpunkten (200 m x 200 m) zahlreiche Parameter der Waldstruktur erfassen (z. B. Totholzmenge, Brusthöhendurchmesser der umgebenden Bäume, Baumartenzusammensetzung). Nach Interpolation der Punkt-Daten und Auswertung der eigens dafür erstellten Karten zeigte sich, dass der oben beschriebene Einfluss lokaler Mulmhöhleneigenschaften auf die Artenvielfalt in den Höhlen immer auch von der Waldstruktur des betreffenden Gebietes abhängt. In den Waldgebieten mit einem höheren Anteil an Laubbäumen (Ebrach und Kelheim) war der Einfluss der lokalen Mulmhöhleneigenschaften ausgeprägter als in dem von Nadelbäumen dominierten Forstbetrieb Fichtelberg. In Fichtelberg gab es nur vereinzelte Laubholz-Mulmhöhlen. Sind Mulmhöhlen in einem Gebiet selten und isoliert, scheint die Qualität der einzelnen Höhlen kaum noch eine Rolle zu spielen – Mulmhöhlenbewohner nehmen, was sie kriegen können. Dementsprechend beeinflusste im Nadelwald einzig der Anteil an Buchen in der näheren Umgebung der untersuchten Mulmhöhlen die Artenvielfalt in den Höhlen positiv (Abbildung 2). Da Buchen im Forstbetrieb Fichtelberg zumeist isoliert in einer Umgebung aus Nadelbäumen stehen, war das Vorhandensein weiterer Buchen im näheren Umkreis der Höhlenbäume (bis zu einem Radius von 100 m) der wichtigste Einflussfaktor für mulmhöhlenbewohnende Käfer in diesem Waldgebiet.

### Totholz ist nicht gleich Totholz

Im Steigerwald (Forstbetrieb Ebrach), dem Gebiet mit dem höchsten Laubholzanteil in unserer Studie, hatte neben den lokalen Mulmhöhleneigenschaften vor allem die Totholzmenge in der Umgebung der Mulmhöhlen (bis zu einem Radius von 100 m) einen positiven Einfluss auf die Artenvielfalt in den Höhlen (Abbildung 2). Dies könnte auf den großen Anteil an Totholzgeneralisten unter den Käfern in den Höhlen zurückzuführen sein, die im Gegensatz zu den Mulmhöhlenspezialisten vielfältige Totholzstrukturen als Lebensraum nutzen können und von einem größeren Totholzangebot in der Umgebung profitieren. In Fichtelberg und Kelheim, die geringere Laubbaumanteile aufweisen, ließ sich dagegen kein Zusammenhang zwischen der Totholzmenge in der näheren Umgebung und der Käferartenvielfalt in den Höhlen nachweisen. Die Bedeutung von Totholz für eine artenreiche xylobionte Insektenfauna in Wäldern wurde bereits vielfältig beschrieben (Gossner et al. 2013; Müller et al. 2015; Seibold & Thorn 2018). Dabei wurde festgestellt, dass neben einer hinreichenden Menge an Totholz auch die Zusammensetzung des Totholzes in Bezug auf Baumart, Durchmesser, Zersetzungsgrad oder Sonnenexposition von großer Bedeutung für die xylobionte Artenvielfalt war (Sverdrup-Thygeson et al. 2014; Seibold et al. 2016). Insekten, die Mulmhöhlen besiedeln, profitieren in der Regel nicht von Nadelbaumtotholz, sondern ausschließlich von Laubbaumtotholz. Dies erklärt, warum in unserer Studie kein Zusammenhang bestand zwischen der Totholzmenge im Forstbetrieb Fichtelberg und der Artenvielfalt in den Mulmhöhlen.

### Einfluss der Landschaftsstruktur auf Mulmhöhlenbewohner

Neben den lokalen Mulmhöhleneigenschaften und der Waldstruktur (im Umkreis bis 500 m) wurde auch der Einfluss der Landschaftsstruktur auf größeren räumlichen Skalen bis 5.000 m um die Mulmhöhlen untersucht. Anhand von Satellitendaten wurde das Verhältnis von Habitat (Laubwald) zu Nichthabitat (Nadelwald und Offenland) in der die Mulmhöhlen umgebenden Landschaft analysiert. Dabei konnten wir zeigen, dass der Einfluss der Landschaftsstruktur auf die Artenvielfalt in den Mulmhöhlen deutlich geringer ausfällt als der Einfluss der lokalen Mulmhöhleneigenschaften oder von Waldstrukturelementen wie z. B. der Menge an Totholz. Bemerkenswert war allerdings, dass der Einfluss der Landschaftsstruktur bei den Rote-Liste-Arten stärker ausgeprägt war. Folglich reagieren gefährdete xylobionte Käferarten sensibler auf das Habitatangebot der umgebenden Landschaft als nicht gefährdete Arten. Für äußerst seltene »Urwaldreliktarten« (in unserer Studie der Schnellkäfer *Crepidophorus mutilatus*) ist bekannt, dass sie Lebensräume mit hochwertiger Habitatausstattung benötigen (Müller et al. 2005).

### Geringe Ausbreitungsfähigkeit von Mulmhöhlenspezialisten?

Die Ausbreitungsfähigkeit der meisten mulmhöhlenbewohnenden Käferarten ist noch unbekannt (Feldhaar & Schauer 2018). Im Rahmen unserer Studie führten wir deshalb für zwei ausgewählte xylobionte Käferarten populationsgenetische Analysen durch. Die zwei Mulmhöhlenspezialisten, der Kammkäfer *Eucnemis capucina* und der Kurzflügelkäfer *Hesperus rufipennis,* wiesen – anders als bei zuvor von uns populationsgenetisch untersuchten Totholzgeneralisten – bereits innerhalb eines Waldgebiets wie dem Forstbetrieb Ebrach eine deutliche genetische Strukturierung auf. Diese könnte einerseits durch ein geringes Ausbreitungsvermögen der Käfer, die an das langlebige Habitat Mulmhöhle angepasst sind, bedingt sein. Andererseits weisen gerade solche Spezialisten häufig auch eine sehr kleine Populationsgröße auf, die zu ähnlichen Mustern führen würde.

**6** **Der Autor beim Anbringen einer höher gelegenen Emergenzfalle an einer Rotbuche im Forstbetrieb Kelheim. Höhleneingang etwa 350 cm über dem Waldboden.** Foto: Vanilla Mertl, Universität Bayreuth

### Fazit

Als Konsequenz der Studie für die forstliche Praxis ergeben sich der Schutz und Erhalt von jeder sich entwickelnden und bestehenden Mulmhöhle, da jede dieser Höhlen in ihrem spezifischen Aufbau und ihrer Ausgestaltung eine einzigartige Bandbreite an wertvollen Kleinsthabitaten enthält (Siitonen 2012; Micó 2018). Angesichts der Seltenheit von Mulmhöhlen in Wirtschaftswäldern und der sehr unterschiedlichen Habitatansprüche ihrer Bewohner sollten sämtliche bestehenden Mulmhöhlen geschützt werden. Darüber hinaus sollten im Hinblick auf die jahrzehntelange Entwicklungszeit von Mulmhöhlen alle Bäume bewahrt werden, die Strukturen (z. B. großflächige Rindenverletzungen, Astabbrüche) enthalten, aus denen sich Mulmhöhlen entwickeln könnten.

Die Studie belegt, dass neben der Qualität der einzelnen Mulmhöhlen auch die Waldstruktur von Bedeutung für die Artenvielfalt der Mulmhöhlenbewohner ist. Folglich ist auch die Anreicherung von Totholz in Wirtschaftswäldern förderlich für den Schutz von Lebensgemeinschaften in Mulmhöhlen (Gossner et al 2013; Müller et al. 2015). Insbesondere sollte Totholz von Laubbaumarten angereichert werden, da xylobionte Käfer nicht nur auf die Menge, sondern auch auf die Baumart sowie den Durchmesser, den Zersetzungsgrad und die Sonnenexposition von Totholz sensibel reagieren (Sverdrup-Thygeson et al. 2014; Seibold et al. 2016).

**7** **Der Kurzflügelkäfer *Hesperus rufipennis* ist ein Mulmhöhlenspezialist und eine von zwei xylobionten Käferarten, die im Rahmen der Studie populationsgenetisch untersucht wurde.** Foto: Per Hoffmann Olsen, www.insects.at

Darüber hinaus hat sich die Baumartenzusammensetzung des jeweiligen Waldgebiets als sehr einflussreich für die xylobionte Artenvielfalt in Mulmhöhlen erwiesen. Deshalb würde auch eine Erhöhung des Laubbaumanteils in nadelholzdominierten Wirtschaftswäldern helfen, die Artenvielfalt xylobionter Käfer in Mulmhöhlen zu erhöhen.

### Zusammenfassung

**Im Rahmen der vorgestellten Studie wurden die Auswirkungen der Landschafts- und Waldstruktur auf die Artenvielfalt von Arthropoden in Mulmhöhlen sowie deren Ausbreitungsdistanzen untersucht. Dies erfolgte unter anderem mit Hilfe von Forstinventur- und Fernerkundungsdaten auf größeren räumlichen Skalen. Die Studie zeigt, dass für die Artenvielfalt in den Mulmhöhlen insbesondere die Qualität der einzelnen Mulmhöhlen, die Waldstruktur sowie die Baumartenzusammensetzung von Bedeutung sind. Da Mulmhöhlen Schlüsselstrukturen für eine hohe Artenvielfalt im Wald darstellen, sollte besonderes Augenmerk auf den Schutz und Erhalt dieses Lebensraums gelegt werden.**

### Projekt

Das Projekt »Arthropodengemeinschaften in Mulmhöhlen im Landschaftskontext: Einfluss der Wald- und der Landschaftsstruktur auf Diversität und Ausbreitungsdistanzen im regionalen Vergleich (L58)« (Laufzeit: 01.04.1918–31.12.2021) wurde, ebenso wie das Vorgängerprojekt L56, durch das Bayerische Staatsministerium für Ernährung, Landwirtschaft und Forsten sowie die Oberfrankenstiftung finanziert.

### Literatur

Das Literaturverzeichnis finden Sie unter *www.lwf.bayern.de* in der Rubrik »Publikationen«.

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**Table A1. Species richness of saproxylic beetles and threatened saproxylic beetles in the tree hollows, and parameters of the examined tree hollows, hollow trees and surrounding forest structure at different spatial scales in the Ebrach study region.** SR = species richness of saproxylic beetles, RL = species richness of threatened saproxylic beetles. Parameters of tree hollows: H.a.s.l. = height above sea level, Volume = hollow volume, Entrance = size of the entrance, Height = height above ground, Decomp. = stage of decomposition, Temp. = temperature inside the hollows. Parameters of hollow trees: DBH = diameter at breast height. Parameters of surrounding forest structure: Hollows = number of tree hollows, Structures = number of microhabitat structures, DW (FI) = dead wood volume, DBH (FI) = average diameter at breast height of deciduous trees, CORINE = habitat proportion.

| ID | Latitude | Longitude | SR | RL | H.a.s.l. [m] | Volume [cm$^3$] | Entrance [cm$^2$] | Height [cm] | Decomp. | Temp. [°C] | DBH [cm] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| B08 | 49.92703 | 10.52274 | 14 | 10 | 425 | 277088.47 | 2639 | 197 | 2 | 17.22 | 65 |
| B11 | 49.94888 | 10.49417 | 18 | 4 | 406 | 10602.88 | 230 | 101 | 3 | 17.03 | 28 |
| B14 | 49.94598 | 10.52679 | 12 | 2 | 384 | 452.39 | 105 | 248 | 3 | 17.84 | 27 |
| B17 | 49.90103 | 10.49744 | 7 | 1 | 395 | 2657.79 | 664 | 40 | 4 | 17.67 | 61 |
| B20 | 49.92438 | 10.569 | 7 | 0 | 473 | 4423.36 | 630 | 87 | 3 | NA | 51 |
| B22 | 49.86128 | 10.53399 | 14 | 8 | 413 | 107010.5 | 2730 | 0 | 2 | 17.45 | 73 |
| B23 | 49.86003 | 10.5431 | 16 | 3 | 408 | 280230.06 | 1365 | 0 | 1 | 16.73 | 73 |
| B27 | 49.85865 | 10.54345 | 15 | 7 | 407 | NA | 1440 | 0 | 1 | 15.89 | 75 |
| B29 | 49.85439 | 10.5647 | 11 | 2 | 324 | 71675.44 | 630 | 137 | 2 | 15.82 | 85 |
| B31 | 49.84724 | 10.53889 | 6 | 0 | 389 | 2650.72 | 649 | 230 | 4 | 15.61 | 34 |
| B37 | 49.86119 | 10.50587 | 18 | 9 | 358 | 150598.53 | 11200 | 0 | 1 | 16.38 | 95 |
| B38 | 49.86663 | 10.48905 | 5 | 1 | 392 | 3926.99 | 1350 | 5 | 2 | NA | 32 |
| B40 | 49.85947 | 10.4709 | 13 | 6 | 392 | 65002.69 | 2100 | 0 | 2 | 15.27 | 72 |
| S01 | 49.96484 | 10.58274 | 25 | 8 | 439 | 40840.7 | 1980 | 15 | 1 | 18.73 | 72 |
| S02 | 49.97073 | 10.5858 | 9 | 0 | 342 | 367.57 | 400 | 174 | 3 | 18.67 | 49 |
| S03 | 49.97005 | 10.60026 | 21 | 5 | 325 | 49480.08 | 480 | 0 | 2 | 17.05 | 42 |
| S04 | 49.96422 | 10.60722 | 4 | 0 | 366 | 25220.71 | 875 | 0 | 3 | 19.8 | 26 |
| S05 | 49.951964 | 10.66527 | 12 | 4 | 329 | 3534.29 | 280 | 6 | 3 | NA | 20 |
| S06 | 49.952108 | 10.679619 | 12 | 0 | 340 | 24555.47 | 5250 | 0 | 2 | NA | 20 |
| S07 | 49.949421 | 10.68131 | 6 | 3 | 378 | 14202.35 | 102 | 173 | 4 | NA | 32 |
| S09 | 49.92509 | 10.58882 | 12 | 2 | 459 | 188495.56 | 250 | 10 | 2 | NA | 70 |
| S10 | 49.92484 | 10.58827 | 12 | 4 | 476 | 35732.47 | 552 | 23 | 2 | NA | 35 |
| S11 | 49.92028 | 10.58476 | 21 | 4 | 420 | 5407.47 | 350 | 0 | 3 | NA | 26 |
| S12 | 49.9129 | 10.59961 | 18 | 3 | 434 | 12959.07 | 1062 | 17 | 2 | NA | 31 |
| S13 | 49.90954 | 10.62199 | 9 | 0 | 392 | 244247.05 | 2405 | 31 | 2 | NA | 72 |
| S14 | 49.89437 | 10.64173 | 21 | 1 | 371 | 2403.32 | 1080 | 0 | 2 | NA | 25 |
| S15 | 49.87724 | 10.45285 | 6 | 2 | 464 | 27488.94 | 1330 | 205 | 3 | 15.91 | 70 |
| S16 | 49.88192 | 10.4408 | 13 | 2 | 474 | 53014.38 | 34 | 30 | NA | 14.8 | 23 |
| S17 | 49.8772 | 10.44959 | 16 | 2 | 442 | 30787.61 | 726 | 61 | 4 | NA | 78 |
| S19 | 49.83489 | 10.49852 | 18 | 3 | 399 | 50265.48 | 1520 | 5 | 3 | 15.14 | 66 |
| S20 | 49.83028 | 10.51431 | 17 | 4 | 369 | 40212.39 | 480 | 0 | 2 | 16.49 | 34 |
| S21 | 49.83304 | 10.53285 | 8 | 1 | 350 | 49087.39 | 60 | 15 | 2 | 14.67 | 37 |
| S22 | 49.79998 | 10.53223 | 10 | 3 | 373 | 33929.2 | 492 | 0 | 3 | 16.54 | 24 |
| S23 | 49.81817 | 10.56309 | 14 | 4 | 361 | 8708.49 | 1309 | 250 | 3 | 17.03 | 52 |
| S24 | 49.79878 | 10.56649 | 10 | 2 | 420 | 42411.5 | 108 | 57 | 2 | 16.74 | 73 |
| S25 | 49.79651 | 10.57759 | 8 | 0 | 429 | 11058.41 | 6600 | 19 | 2 | 18.01 | 58 |
| S26 | 49.80582 | 10.60694 | 12 | 1 | 390 | 19085.18 | 854 | 99 | 2 | 18 | 47 |
| S27 | 49.80043 | 10.62686 | 8 | 0 | 337 | 13069.03 | 504 | 38 | 3 | 15.74 | 51 |
| S28 | 49.7542 | 10.59715 | 13 | 1 | 361 | 75398.22 | 1040 | 0 | 2 | 17.37 | 61 |
| S29 | 49.75142 | 10.58613 | 12 | 0 | 390 | 6652.32 | 140 | 42 | NA | 16.44 | 36 |
| S30 | 49.77217 | 10.686 | 12 | 2 | 389 | 5654.87 | 6000 | 0 | 1 | 18.48 | 80 |
| S31 | 49.76706 | 10.66903 | 30 | 4 | 326 | 8042.48 | 14220 | 0 | 2 | 18.19 | 71 |
| S32 | 49.87007 | 10.606979 | 18 | 5 | 374 | 18582.52 | 1100 | 34 | 2 | 18.91 | 24 |
| S33 | 49.852881 | 10.625037 | 29 | 5 | 339 | 22564.49 | 1230 | 0 | 2 | 17.03 | 62 |
| S36 | 49.89048 | 10.68747 | 10 | 0 | 420 | 31855.75 | 810 | 124 | 3 | 16.9 | 76 |
| S45 | 49.85198 | 10.50643 | 2 | 1 | 419 | 31777.21 | 800 | 0 | 2 | 15.16 | 52 |
| S46 | 49.93534 | 10.47313 | 23 | 8 | 480 | 76340.7 | 2556 | 0 | 1 | 18.09 | 48 |
| S47 | 49.92897 | 10.50324 | 12 | 2 | 399 | 15020.74 | 495 | 5 | 3 | 15.57 | 48 |
| S48 | 49.94131 | 10.48987 | 9 | 2 | 482 | 23750.44 | 1700 | 10 | 3 | 16.51 | 48 |
| S49 | 49.92608 | 10.51782 | 12 | 2 | 440 | 75398.22 | 1900 | 67 | 2 | 16.51 | 46 |

| ID | Hollows (r = 30 m) | Structures (r = 30 m) | DW (FI) (r = 50 m) [m$^3$/ha] | DW (FI) (r = 100 m) [m$^3$/ha] | DW (FI) (r = 200 m) [m$^3$/ha] | DW (FI) (r = 300 m) [m$^3$/ha] | DW (FI) (r = 500 m) [m$^3$/ha] | DBH (FI) (r = 50 m) [cm] |
|---|---|---|---|---|---|---|---|---|
| B08 | 0 | 5 | 22.14 | 22.02 | NA | NA | NA | 21.88 |
| B11 | 1 | 4 | 26.58 | 29.67 | 33.64 | 28.89 | NA | 23.62 |
| B14 | 0 | 2 | 21.03 | 21.74 | 22.69 | 22.34 | 21.45 | 21.36 |
| B17 | 3 | 4 | 19.04 | 19.15 | 19.16 | 19.08 | 17.74 | 24.18 |
| B20 | 2 | 5 | 20.41 | 19.25 | 19.7 | 23.29 | 23.27 | 16.69 |
| B22 | 0 | 2 | 4.66 | 5.03 | 7.01 | 9.02 | NA | 19.24 |
| B23 | 1 | 2 | 23.51 | 22.11 | NA | NA | NA | 17.89 |
| B27 | 4 | 3 | 5.87 | 25.61 | 43.69 | 47.66 | 39.47 | 18.76 |
| B29 | 0 | 1 | 27.94 | 28.93 | 34.49 | 34.85 | 30.65 | 17.27 |
| B31 | 2 | 1 | 43.96 | 43.43 | 40.03 | 32.75 | 23.18 | 16.06 |
| B37 | 1 | 4 | 19.46 | 29.86 | 40.49 | 39.79 | 33.77 | 19.5 |
| B38 | 2 | 4 | 14.83 | 13.18 | 16.82 | 20.1 | 19.91 | 22.5 |
| B40 | 0 | 7 | 21.92 | 21.98 | 26.58 | 32.74 | 28.76 | 19.76 |
| S01 | 0 | 10 | 6.76 | 6.72 | 7.49 | 8.43 | 10.83 | 15.9 |
| S02 | 0 | 3 | 7.84 | 8.35 | 9.27 | 10.75 | NA | 12.9 |
| S03 | 3 | 7 | 23.33 | 23.72 | 25.36 | 26.84 | 24.21 | 15.85 |
| S04 | 1 | 5 | 7.85 | 7.72 | 7.26 | 7.58 | NA | 15.78 |
| S05 | 0 | 6 | 6.31 | 8.7 | 12.03 | NA | NA | 17.37 |
| S06 | 4 | 2 | 5.81 | 6.05 | 7.1 | 8.23 | 12.92 | 12.49 |
| S07 | 0 | 6 | 11.32 | 11.52 | NA | NA | NA | 16.85 |
| S09 | 3 | 7 | 21.13 | NA | NA | NA | NA | 16.35 |
| S10 | 0 | 5 | 23.28 | 25.74 | 26.65 | 26.54 | NA | 16.4 |
| S11 | 1 | 6 | 33.79 | 34.25 | 32.92 | NA | NA | 15.83 |
| S12 | 1 | 4 | 40.72 | 41.53 | 42.53 | NA | NA | 15.55 |
| S13 | 0 | 2 | 43.82 | 43.97 | 43.44 | 40.93 | 27.88 | 16.14 |
| S14 | 2 | 6 | 9.14 | 8.85 | NA | NA | NA | 17.86 |
| S15 | 0 | 3 | 35.23 | 34.66 | NA | NA | NA | 18.85 |
| S16 | 2 | 7 | 30.73 | 28.55 | NA | NA | NA | 16.62 |
| S17 | 2 | 5 | 32.54 | 33.79 | 33.57 | 32.24 | 28.24 | 18.34 |
| S19 | 1 | 3 | 53.09 | 47.91 | 43.67 | NA | NA | 19.38 |
| S20 | 1 | 3 | 14.66 | 14.53 | 15.4 | 18.32 | 22.67 | 17.43 |
| S21 | 1 | 4 | 16.78 | 19.06 | 20.58 | 21.39 | 19.05 | 19.05 |
| S22 | 3 | 2 | 15.37 | 16.78 | 21.2 | 23.66 | 25.79 | 19.91 |
| S23 | 1 | 3 | 17.1 | 16.73 | NA | NA | NA | 21.55 |
| S24 | 0 | 2 | 20.59 | 20.02 | 18.76 | 18.94 | 19.76 | 20.55 |
| S25 | 0 | 6 | 5.78 | 6.31 | 7.35 | 7.88 | NA | 26.15 |
| S26 | 1 | 2 | 10.67 | 10.05 | NA | NA | NA | 26.98 |
| S27 | 0 | 1 | 8.62 | 10.26 | NA | NA | NA | 19.28 |
| S28 | 0 | 4 | 16.97 | 16.9 | 16.25 | NA | NA | 25.05 |
| S29 | 0 | 2 | 10.95 | 10.87 | NA | NA | NA | 22.17 |
| S30 | 1 | 0 | 7.99 | 8.03 | 8.91 | 9.45 | NA | 29.4 |
| S31 | 0 | 2 | 9.74 | 9.56 | NA | NA | NA | 28.34 |
| S32 | 1 | 8 | 40.36 | 39.55 | NA | NA | NA | 26.01 |
| S33 | 1 | 1 | 36.18 | 31.34 | 26.1 | 24.99 | 23.97 | 23.34 |
| S36 | 1 | 2 | 24.52 | 26.21 | 26.98 | 27.09 | 29.2 | 23.72 |
| S45 | 0 | 1 | 35.5 | 37.83 | 36.87 | 31.5 | NA | 15.76 |
| S46 | 0 | 10 | 13.31 | 13.01 | 13.37 | 14.04 | 15.11 | 17.05 |
| S47 | 2 | 11 | 16.26 | 16.18 | 16.27 | 16.49 | 17.35 | 19.33 |
| S48 | 1 | 3 | 6.03 | 6.41 | 6.44 | 6.48 | 7.16 | 22.72 |
| S49 | 4 | 9 | 19.34 | 19.99 | 20.81 | 21.49 | 23.66 | 21.58 |

| ID | DBH (FI) (r = 100 m) [cm] | DBH (FI) (r = 200 m) [cm] | DBH (FI) (r = 300 m) [cm] | DBH (FI) (r = 500 m) [cm] | CORINE (r = 300 m) | CORINE (r = 500 m) | CORINE (r = 1000 m) | CORINE (r = 1500 m) |
|---|---|---|---|---|---|---|---|---|
| B08 | 21.96 | NA | NA | NA | 0.8801 | 0.8735 | 0.8376 | 0.8567 |
| B11 | 23.66 | 23.68 | 23.62 | NA | 0.87 | 0.8293 | 0.8244 | 0.7357 |
| B14 | 21.31 | 21.32 | 21.36 | 21.49 | 0.8162 | 0.9111 | 0.8873 | 0.8612 |
| B17 | 24.27 | 24.27 | 24.2 | 24.09 | 0.9352 | 0.8908 | 0.8018 | 0.7336 |
| B20 | 16.69 | 16.68 | 16.67 | 16.67 | 0.9965 | 0.9757 | 0.8861 | 0.8001 |
| B22 | 19.29 | 19.11 | 18.78 | NA | 0.983 | 0.9739 | 0.8509 | 0.8151 |
| B23 | 17.85 | NA | NA | NA | 0.9504 | 0.9488 | 0.9441 | 0.88 |
| B27 | 18.77 | 18.59 | 18.35 | 18.01 | 0.9989 | 0.9718 | 0.9466 | 0.905 |
| B29 | 17.18 | 17.03 | 16.96 | 17.58 | 0.7984 | 0.8775 | 0.8313 | 0.7252 |
| B31 | 16.15 | 16.2 | 16.35 | 16.56 | 0.9543 | 0.918 | 0.8804 | 0.8469 |
| B37 | 19.55 | 19.79 | 20.06 | 20.36 | 0.7966 | 0.8253 | 0.8176 | 0.8113 |
| B38 | 22.45 | 22.43 | 22.21 | 21.64 | 0.7922 | 0.7962 | 0.8578 | 0.8615 |
| B40 | 19.76 | 19.96 | 20.43 | 21.33 | 0.854 | 0.8273 | 0.8527 | 0.8057 |
| S01 | 16.04 | 16.29 | 16.31 | 15.82 | 0.9908 | 0.9934 | 0.9309 | 0.7078 |
| S02 | 13.16 | 13.36 | 13.69 | NA | 0.9813 | 0.8564 | 0.764 | 0.6451 |
| S03 | 15.68 | 15.48 | 15.29 | 15.31 | 0.9862 | 0.8611 | 0.8288 | 0.684 |
| S04 | 15.7 | 15.53 | 15.35 | NA | 0.9001 | 0.7743 | 0.749 | 0.7208 |
| S05 | 17.39 | 17.3 | NA | NA | 0.7813 | 0.7461 | 0.7195 | 0.553 |
| S06 | 12.85 | 13.73 | 14.75 | 16.21 | 0.7253 | 0.7631 | 0.7098 | 0.5441 |
| S07 | 16.89 | NA | NA | NA | 0.8488 | 0.7348 | 0.638 | 0.5398 |
| S09 | NA | NA | NA | NA | 0.7488 | 0.7596 | 0.7367 | 0.6945 |
| S10 | 16.41 | 16.41 | 16.42 | NA | 0.7841 | 0.767 | 0.743 | 0.7039 |
| S11 | 15.82 | 15.81 | NA | NA | 0.9746 | 0.8064 | 0.7666 | 0.7763 |
| S12 | 15.67 | 15.65 | NA | NA | 0.8554 | 0.6463 | 0.5503 | 0.5356 |
| S13 | 16.08 | 16.21 | 16.58 | 17.01 | 0.6576 | 0.7634 | 0.6876 | 0.4965 |
| S14 | 17.76 | NA | NA | NA | 0.3012 | 0.2599 | 0.243 | 0.222 |
| S15 | 18.47 | NA | NA | NA | 0.9111 | 0.9284 | 0.8596 | 0.784 |
| S16 | 16.68 | NA | NA | NA | 0.9996 | 0.9888 | 0.8255 | 0.7676 |
| S17 | 18.8 | 18.79 | 18.62 | 18.56 | 0.9358 | 0.9477 | 0.7991 | 0.7694 |
| S19 | 19.34 | 19.37 | NA | NA | 0.834 | 0.6048 | 0.4786 | 0.3996 |
| S20 | 17.49 | 17.67 | 17.71 | 17.79 | 0.8749 | 0.8061 | 0.7547 | 0.7095 |
| S21 | 19.51 | 19.33 | 19.1 | 18.81 | 0.7699 | 0.621 | 0.6743 | 0.7147 |
| S22 | 19.88 | 19.85 | 19.79 | 19.69 | 0.9593 | 0.8708 | 0.7128 | 0.5276 |
| S23 | 21.8 | NA | NA | NA | 0.7353 | 0.622 | 0.4582 | 0.401 |
| S24 | 20.54 | 20.65 | 20.85 | 21.25 | 0.7748 | 0.806 | 0.6767 | 0.5547 |
| S25 | 25.92 | 25.78 | 25.48 | NA | 0.9005 | 0.7323 | 0.5522 | 0.4853 |
| S26 | 26.8 | NA | NA | NA | 0.6133 | 0.4997 | 0.6091 | 0.59 |
| S27 | 19.67 | NA | NA | NA | 0.6073 | 0.5294 | 0.4675 | 0.4073 |
| S28 | 25.35 | 25.01 | NA | NA | 0.6274 | 0.463 | 0.251 | 0.1671 |
| S29 | 21.86 | NA | NA | NA | 0.2605 | 0.2199 | 0.2429 | 0.1799 |
| S30 | 29.13 | 28.83 | 28.7 | NA | 0.6429 | 0.5618 | 0.2799 | 0.2365 |
| S31 | 28.11 | NA | NA | NA | 0.4189 | 0.359 | 0.2091 | 0.1751 |
| S32 | 25.79 | NA | NA | NA | 0.6004 | 0.4409 | 0.2806 | 0.2389 |
| S33 | 23.55 | 24.05 | 24.8 | 25.74 | 0.5634 | 0.5913 | 0.5927 | 0.4793 |
| S36 | 23.91 | 24.02 | 23.98 | 23.79 | 0.6628 | 0.6009 | 0.4707 | 0.4043 |
| S45 | 16.1 | 16.94 | 17.8 | NA | 0.9883 | 0.902 | 0.712 | 0.6696 |
| S46 | 17.4 | 17.7 | 17.96 | 18.92 | 0.9704 | 0.9341 | 0.9161 | 0.9372 |
| S47 | 19.31 | 19.66 | 20.01 | 20.38 | 0.8724 | 0.8953 | 0.898 | 0.8977 |
| S48 | 22.89 | 22.92 | 22.72 | 22.47 | 0.9831 | 0.939 | 0.8625 | 0.872 |
| S49 | 21.45 | 21.42 | 21.58 | 21.96 | 0.9539 | 0.9273 | 0.8743 | 0.8622 |

| ID | CORINE (r = 2000 m) | CORINE (r = 3000 m) | CORINE (r = 4000 m) | CORINE (r = 5000 m) |
|---|---|---|---|---|
| B08 | 0.8442 | 0.8153 | 0.8028 | 0.6945 |
| B11 | 0.7132 | 0.6893 | 0.6321 | 0.5534 |
| B14 | 0.8578 | 0.7439 | 0.6516 | 0.6113 |
| B17 | 0.6537 | 0.6577 | 0.6914 | 0.6869 |
| B20 | 0.7244 | 0.6786 | 0.6366 | 0.6019 |
| B22 | 0.8158 | 0.7006 | 0.5883 | 0.5337 |
| B23 | 0.8066 | 0.6751 | 0.5508 | 0.4988 |
| B27 | 0.8189 | 0.6814 | 0.5545 | 0.4954 |
| B29 | 0.6401 | 0.5268 | 0.4708 | 0.4358 |
| B31 | 0.7828 | 0.7141 | 0.5953 | 0.5078 |
| B37 | 0.7873 | 0.6848 | 0.6465 | 0.6307 |
| B38 | 0.8275 | 0.6759 | 0.6444 | 0.6362 |
| B40 | 0.797 | 0.6977 | 0.5977 | 0.5717 |
| S01 | 0.5843 | 0.4699 | 0.4572 | 0.463 |
| S02 | 0.5231 | 0.4167 | 0.3944 | 0.4104 |
| S03 | 0.6015 | 0.4706 | 0.4078 | 0.4065 |
| S04 | 0.6637 | 0.5463 | 0.458 | 0.4271 |
| S05 | 0.4641 | 0.3938 | 0.3669 | 0.3493 |
| S06 | 0.4401 | 0.3218 | 0.3267 | 0.3189 |
| S07 | 0.416 | 0.3222 | 0.3149 | 0.3097 |
| S09 | 0.6644 | 0.5996 | 0.5874 | 0.5466 |
| S10 | 0.6694 | 0.5993 | 0.5883 | 0.5465 |
| S11 | 0.6989 | 0.5955 | 0.5551 | 0.5282 |
| S12 | 0.5916 | 0.5433 | 0.4399 | 0.4239 |
| S13 | 0.4249 | 0.3817 | 0.3596 | 0.3474 |
| S14 | 0.2333 | 0.2331 | 0.2526 | 0.2752 |
| S15 | 0.7659 | 0.7331 | 0.6181 | 0.5277 |
| S16 | 0.7646 | 0.6459 | 0.533 | 0.489 |
| S17 | 0.7727 | 0.7164 | 0.5964 | 0.5165 |
| S19 | 0.4461 | 0.5764 | 0.6051 | 0.5833 |
| S20 | 0.6134 | 0.5707 | 0.5704 | 0.5652 |
| S21 | 0.7076 | 0.6244 | 0.5819 | 0.5383 |
| S22 | 0.4547 | 0.4635 | 0.4139 | 0.3802 |
| S23 | 0.4022 | 0.4655 | 0.4689 | 0.4649 |
| S24 | 0.4863 | 0.4514 | 0.4019 | 0.3587 |
| S25 | 0.5086 | 0.4472 | 0.3747 | 0.3275 |
| S26 | 0.4791 | 0.3682 | 0.319 | 0.2927 |
| S27 | 0.3896 | 0.3376 | 0.2745 | 0.249 |
| S28 | 0.1383 | 0.1247 | 0.1296 | 0.1508 |
| S29 | 0.1347 | 0.1161 | 0.1346 | 0.1381 |
| S30 | 0.1918 | 0.1471 | 0.1317 | 0.1195 |
| S31 | 0.1645 | 0.1469 | 0.1364 | 0.1288 |
| S32 | 0.2406 | 0.2533 | 0.2792 | 0.3266 |
| S33 | 0.387 | 0.2636 | 0.222 | 0.2292 |
| S36 | 0.3282 | 0.2138 | 0.1713 | 0.1774 |
| S45 | 0.6787 | 0.689 | 0.6765 | 0.6191 |
| S46 | 0.9159 | 0.7785 | 0.6498 | 0.5731 |
| S47 | 0.8876 | 0.8763 | 0.8032 | 0.6858 |
| S48 | 0.8661 | 0.7935 | 0.7048 | 0.6046 |
| S49 | 0.8596 | 0.8243 | 0.8024 | 0.6999 |

**Table A2. Species richness of saproxylic beetles and threatened saproxylic beetles in the tree hollows, and parameters of the examined tree hollows, hollow trees and surrounding forest structure at different spatial scales in the Fichtelberg study region.** SR = species richness of saproxylic beetles, RL = species richness of threatened saproxylic beetles. Parameters of tree hollows: H.a.s.l. = height above sea level, Volume = hollow volume, Entrance = size of the entrance, Height = height above ground, Decomp. = stage of decomposition, Temp. = temperature inside the hollows. Parameters of hollow trees: DBH = diameter at breast height. Parameters of surrounding forest structure: Hollows = number of tree hollows, Structures = number of microhabitat structures, DW (FI) = dead wood volume, DBH (FI) = average diameter at breast height of deciduous trees, Proportion beech (FI) = proportion of beech trees, CORINE = habitat proportion.

| ID | Latitude | Longitude | SR | RL | H.a.s.l. [m] | Volume [cm$^3$] | Entrance [cm$^2$] | Height [cm] | Decomp. | Temp. [°C] | DBH [cm] | Hollows (r = 30 m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| F02 | 50.04549 | 11.72547 | 10 | 5 | 525 | 13391.82 | 540 | 0 | 2 | 14.62 | 78 | 1 |
| F06 | 50.03904 | 11.73343 | 3 | 0 | 592 | 11561.06 | 279 | 0 | 2 | 14.33 | 46 | 1 |
| F08 | 50.02472 | 11.74039 | 2 | 0 | 731 | 15904.31 | 240 | 19 | 1 | 14.06 | 33 | 0 |
| F09 | 50.02937 | 11.75666 | 7 | 0 | 800 | 4846.69 | 1980 | 40 | 4 | 13.08 | 29 | 0 |
| F11 | 50.0151 | 11.76588 | 3 | 0 | 760 | 4898.53 | 414 | 14 | 2 | 13.04 | 55 | 0 |
| F12 | 50.01721 | 11.77355 | 6 | 1 | 742 | 3771.48 | 690 | 0 | 3 | 14.87 | 33 | 1 |
| F13 | 50.00486 | 11.73382 | 4 | 0 | 808 | 4005.53 | 517 | 18 | 1 | 14.09 | 50 | 1 |
| F14 | 50.00493 | 11.73967 | 3 | 2 | 763 | 35342.92 | 1400 | 125 | 4 | 14.28 | 85 | 1 |
| F16 | 49.99574 | 11.72123 | 9 | 0 | 728 | 3298.67 | 84 | 40 | 2 | 13.97 | 24 | 0 |
| F18 | 49.99251 | 11.7376 | 7 | 0 | 807 | 7932.52 | 355 | 104 | 1 | 13.7 | 33 | 1 |
| F19 | 49.99243 | 11.72334 | 1 | 0 | 684 | 3141.59 | 60 | 190 | 2 | 14.64 | 28 | 0 |
| F21 | 49.98201 | 11.71837 | 2 | 0 | 606 | 2007.48 | 244 | 58 | 3 | 16.95 | 20 | 1 |
| F22 | 49.98463 | 11.72273 | 8 | 0 | 624 | 21397.39 | 1278 | 0 | 3 | 14.8 | 32 | 0 |
| F23 | 49.97902 | 11.71938 | 13 | 2 | 673 | 10756.81 | 2030 | 0 | 1 | 15.83 | 21 | 0 |
| F24 | 50.03465 | 11.83641 | 1 | 0 | 759 | 294053.07 | 5720 | 0 | 3 | 13.65 | 52 | 1 |
| F25 | 49.99516 | 11.93666 | 3 | 1 | 701 | 10995.57 | 2940 | 0 | 1 | 15.93 | 69 | 1 |
| F26 | 49.99471 | 11.93232 | 2 | 1 | 749 | 16787.89 | 884 | 22 | 3 | 12.89 | 61 | 0 |
| F27 | 50.00937 | 11.93415 | 8 | 0 | 620 | 785.4 | 297 | 0 | 1 | 13.84 | 28 | 2 |
| F28 | 49.99908 | 11.91779 | 3 | 0 | 687 | 22902.21 | 84 | 31 | 3 | 13.08 | 54 | 2 |
| F29 | 50.00012 | 11.90664 | 2 | 0 | 746 | 9954.92 | 750 | 27 | 2 | 13.18 | 86 | 1 |
| F30 | 50.02835 | 11.89894 | 3 | 0 | 679 | 38170.35 | 1875 | 117 | 2 | 16.26 | 85 | 0 |
| F31 | 50.029 | 11.90888 | 3 | 2 | 673 | 86519.46 | 6125 | 0 | 3 | 14.21 | 104 | 0 |
| F33 | 50.04124 | 11.91414 | 7 | 1 | 683 | 106499.99 | 7280 | 0 | 4 | 14.65 | 53 | 0 |
| F34 | 50.0249 | 11.88108 | 4 | 0 | 863 | 229022.1 | 3500 | 0 | 1 | 12.93 | 76 | 1 |
| F35 | 50.01581 | 11.88053 | 2 | 0 | 784 | 69115.04 | 1660 | 43 | 2 | 15.39 | 147 | 0 |
| F36 | 50.03214 | 11.85812 | 4 | 0 | 779 | 21551.33 | 3375 | 36 | 1 | 14.5 | 63 | 2 |
| F37 | 49.99628 | 11.82674 | 2 | 1 | 713 | 2770.88 | 610 | 0 | 1 | 14.46 | 29 | 0 |
| F39 | 49.94863 | 11.83764 | 4 | 0 | 832 | 23532.89 | 160 | 59 | 1 | 12.54 | 57 | 1 |
| F40 | 49.95289 | 11.85681 | 6 | 0 | 801 | 6542.37 | 291 | 42 | NA | 14.74 | 224 | 0 |
| F41 | 49.94146 | 11.88002 | 5 | 0 | 733 | 8293.8 | 1980 | 214 | 4 | 14.54 | 47 | 1 |
| F42 | 49.98488 | 11.79475 | 3 | 0 | 783 | 2375.83 | 90 | 158 | NA | 13.55 | 46 | 2 |
| F44 | 49.96051 | 11.8099 | 10 | 2 | 724 | 61122.83 | 324 | 83 | 2 | 12.93 | 75 | 0 |
| F46 | 49.96926 | 11.77612 | 8 | 2 | 743 | 55292.03 | 480 | 16 | 3 | 13.1 | 99 | 0 |
| F47 | 49.98016 | 11.78172 | 4 | 1 | 676 | 8081.75 | 1260 | 252 | 3 | 15.75 | 58 | 1 |
| F48 | 49.94882 | 11.77125 | 6 | 3 | 573 | 54427.31 | 2227 | 28 | 1 | 15.08 | 150 | 1 |
| F49 | 50.06981 | 11.79183 | 4 | 0 | 768 | 3986.68 | 2256 | 10 | 1 | 14.1 | 32 | 0 |
| F50 | 50.08267 | 11.787 | 4 | 0 | 721 | 4040.87 | 1680 | 0 | 2 | 14.19 | 22 | 1 |
| F51 | 50.0444 | 11.76904 | 4 | 2 | 765 | 6283.19 | 972 | 320 | 2 | 14.41 | 63 | 2 |
| F52 | 50.03389 | 11.78635 | 3 | 1 | 735 | 7068.58 | 427 | 87 | NA | 15.21 | 39 | 0 |
| F53 | 50.0246 | 11.7906 | 3 | 1 | 802 | 56278.49 | 945 | 305 | 3 | 14.07 | 72 | 1 |
| F54 | 50.02048 | 11.82841 | 6 | 1 | 873 | 12440.71 | 1870 | 153 | 2 | 14.4 | 41 | 1 |
| F55 | 50.01249 | 11.97303 | 0 | 0 | 641 | 20910.44 | 295 | 0 | 3 | 13.79 | 37 | 0 |
| F56 | 49.99948 | 11.97115 | 5 | 1 | 717 | 23891.81 | 280 | 74 | 4 | 13.42 | 102 | 1 |

| ID | Structures (r = 30 m) | DW (FI) (r = 50 m) [$m^3$/ha] | DW (FI) (r = 100 m) [$m^3$/ha] | DW (FI) (r = 200 m) [$m^3$/ha] | DW (FI) (r = 300 m) [$m^3$/ha] | DW (FI) (r = 500 m) [$m^3$/ha] | DBH (FI) (r = 50 m) [cm] | DBH (FI) (r = 100 m) [cm] |
|---|---|---|---|---|---|---|---|---|
| F02 | 5 | 16.64 | 16.7 | NA | NA | NA | 37.28 | 37.4 |
| F06 | 4 | 16.89 | 16.59 | 15.73 | 15.32 | 18.38 | 43.62 | 43.65 |
| F08 | 3 | 21.93 | 21.53 | 19.61 | 17.62 | 15.8 | 33.81 | 33.65 |
| F09 | 4 | 44.24 | 43.28 | 38.71 | 33.75 | 27.35 | 37.52 | 37.59 |
| F11 | 3 | 8.54 | 8.77 | 10.53 | 12.8 | NA | 35.12 | 35.31 |
| F12 | 4 | 44.3 | 43.85 | 47.3 | 56.91 | 46.55 | 33.54 | 33.48 |
| F13 | 5 | 17.05 | 16.92 | 17.63 | 18.04 | 15.83 | 25.67 | 25.52 |
| F14 | 7 | 14.39 | 14.38 | 14.45 | NA | NA | 28.22 | 28.5 |
| F16 | 2 | 19.91 | 19.83 | 20.07 | 20.91 | 18.46 | 24.57 | 24.41 |
| F18 | 4 | 18.6 | 18.46 | 17.54 | 16.63 | 18.46 | 28.78 | 28.72 |
| F19 | 1 | 8.91 | 9.48 | 10.13 | NA | NA | 27.29 | 27.17 |
| F21 | 2 | 8.34 | 8.78 | NA | NA | NA | 32.71 | 32.88 |
| F22 | 2 | 8.32 | 8.24 | 8.38 | 8.5 | 9.19 | 29.67 | 29.71 |
| F23 | 5 | 7.22 | 7.34 | 8.06 | 8.46 | NA | 32.71 | 32.74 |
| F24 | 5 | 25.83 | 25.69 | 25.65 | 27.11 | 28.25 | 38.03 | 38.03 |
| F25 | 7 | 16.23 | 16.28 | NA | NA | NA | 39.79 | 39.82 |
| F26 | 6 | 18.34 | 18.33 | 19.46 | 20.15 | 20.35 | 41.2 | 41.25 |
| F27 | 7 | 9.46 | 9.72 | NA | NA | NA | 38.57 | 38.57 |
| F28 | 6 | 15.06 | 14.78 | 14.42 | 15.2 | NA | 36.4 | 37.37 |
| F29 | 4 | 10.53 | 10.41 | 10.47 | 10.71 | 13.58 | 35.12 | 35.12 |
| F30 | 5 | 18.46 | 18.32 | 18.33 | 18.56 | 19.26 | 45.4 | 45.98 |
| F31 | 9 | 18.78 | 19.41 | NA | NA | NA | 51.87 | 51.65 |
| F33 | 5 | 9.74 | 9.92 | 11.3 | 13.14 | NA | 45.81 | 45.38 |
| F34 | 12 | 4.57 | 8.31 | 13.37 | 15.62 | 19.53 | 49.33 | 49.34 |
| F35 | 3 | 11.29 | 10.91 | 11.41 | 13.26 | 16.84 | 35.93 | 35.91 |
| F36 | 3 | 5.38 | 5.75 | 7.04 | 8.34 | 10.26 | 40.31 | 40.74 |
| F37 | 3 | 6.66 | 7.03 | 8.2 | 9.38 | 10.26 | 24.16 | 24.17 |
| F39 | 16 | 9.75 | 9.56 | 9.74 | 10.11 | 10.54 | 32.41 | 32.32 |
| F40 | 5 | 16.11 | 16.13 | 16.05 | 15.19 | 13.53 | 28.25 | 28.05 |
| F41 | 7 | 17.37 | 17.26 | NA | NA | NA | 39.72 | 39.75 |
| F42 | 14 | 8.81 | 8.78 | 10.85 | 12.23 | 14.67 | 33.27 | 33.27 |
| F44 | 4 | 8.13 | 8.09 | NA | NA | NA | 20.15 | 19.85 |
| F46 | 6 | 10.45 | 12.68 | 15.23 | 14.7 | 14.81 | 30.81 | 31.23 |
| F47 | 4 | 13.32 | 13.24 | 13.71 | 14.81 | 16.27 | 34.93 | 35.06 |
| F48 | 15 | 14.79 | 16.6 | 21.45 | NA | NA | 23.75 | 24.03 |
| F49 | 8 | 16.5 | 16.41 | 17.57 | 20.26 | 21.21 | 27.77 | 28.02 |
| F50 | 6 | 18.41 | 17.73 | 15.01 | 12.51 | 10.16 | 30.05 | 30.09 |
| F51 | 16 | 7.47 | 7.47 | 7.45 | 7.68 | 8.09 | 35.85 | 36.05 |
| F52 | 12 | 17.59 | 17.52 | 17.46 | 17.38 | 18.42 | 34.64 | 34.92 |
| F53 | 10 | 23.55 | 24.14 | 25.12 | 25.91 | 23.69 | 42.36 | 42.57 |
| F54 | 9 | 14.47 | 14.52 | 14.31 | 14.71 | 16.79 | 42.12 | 41.97 |
| F55 | 5 | 12.16 | 12.47 | 13.36 | 13.3 | NA | 31.52 | 31.51 |
| F56 | 6 | 47.73 | 48.06 | 43.92 | 35.6 | 25.39 | 20.98 | 21.26 |

| ID | DBH (FI) (r = 200 m) [cm] | DBH (FI) (r = 300 m) [cm] | DBH (FI) (r = 500 m) [cm] | Proportion beech (FI) (r = 50 m) | Proportion beech (FI) (r = 100 m) | Proportion beech (FI) (r = 200 m) | Proportion beech (FI) (r = 300 m) | Proportion beech (FI) (r = 500 m) |
|---|---|---|---|---|---|---|---|---|
| F02 | NA | NA | NA | 81.97 | 80.46 | NA | NA | NA |
| F06 | 43.74 | 43.51 | 43.22 | 35.91 | 39.32 | 49.09 | 53.49 | 55.17 |
| F08 | 33.64 | 33.68 | 34.46 | 41.68 | 41.03 | 39.19 | 37.8 | 37.83 |
| F09 | 37.7 | 38.46 | 39.36 | 49.45 | 49.85 | 50.08 | 49.97 | 49.03 |
| F11 | 35.65 | 35.61 | NA | 44.52 | 44.48 | 44.3 | 43.88 | NA |
| F12 | 33.3 | 33.25 | 33.51 | 41.47 | 41.4 | 41.27 | 41.58 | 47.33 |
| F13 | 25.78 | 26.2 | 26.87 | 32.55 | 32.69 | 32.66 | 32.56 | 32.67 |
| F14 | 28.85 | NA | NA | 30.28 | 30.35 | 30.2 | NA | NA |
| F16 | 24.08 | 24.09 | 24.66 | 56.04 | 55.97 | 55.91 | 55.78 | 54.4 |
| F18 | 28.55 | 28.29 | 28.42 | 32.14 | 32.25 | 32.32 | 32.2 | 32.9 |
| F19 | 26.84 | NA | NA | 44.46 | 44.74 | 45.38 | NA | NA |
| F21 | NA | NA | NA | 43.8 | 43.8 | NA | NA | NA |
| F22 | 29.74 | 29.88 | 30.49 | 38.12 | 38.11 | 38.31 | 38.66 | 39.41 |
| F23 | 32.78 | 32.81 | NA | 48.5 | 48.53 | 48.7 | 48.88 | NA |
| F24 | 38.03 | 38.95 | 40.65 | 59.15 | 59.1 | 59 | 58.71 | 56.08 |
| F25 | NA | NA | NA | 74.81 | 74.63 | NA | NA | NA |
| F26 | 40.98 | 40.65 | 40.47 | 45.05 | 45.64 | 49.16 | 54.29 | 58.8 |
| F27 | NA | NA | NA | 61.29 | 61.37 | NA | NA | NA |
| F28 | 37.67 | 37.84 | NA | 14.93 | 16.46 | 21.78 | 25.37 | NA |
| F29 | 35.38 | 35.68 | 36.96 | 26.43 | 26.6 | 27.33 | 29.01 | 32.46 |
| F30 | 46.89 | 47.7 | 48.06 | 46.7 | 46.8 | 47.3 | 47.76 | 48.78 |
| F31 | NA | NA | NA | 31.66 | 31.65 | NA | NA | NA |
| F33 | 45.36 | 45.68 | NA | 43.83 | 44.9 | 48.5 | 49.71 | NA |
| F34 | 49.02 | 48.36 | 47.45 | 53.52 | 53.92 | 54.66 | 55.17 | 55.67 |
| F35 | 35.86 | 36.63 | 38.58 | 45.56 | 45.77 | 46.49 | 46.81 | 46.64 |
| F36 | 41.03 | 42.22 | 43.61 | 39.77 | 39.78 | 39.89 | 40.12 | 41.98 |
| F37 | 24.23 | 24.58 | 25.04 | 44.21 | 43.95 | 43.27 | 42.6 | 44.63 |
| F39 | 32.41 | 32.54 | 32.99 | 31.16 | 31.21 | 31.26 | 31.08 | 33.56 |
| F40 | 27.8 | 27.92 | 28.29 | 43.5 | 43.45 | 43.19 | 42.92 | 43.41 |
| F41 | NA | NA | NA | 13.07 | 14.85 | NA | NA | NA |
| F42 | 33.36 | 33.11 | 32.33 | 20.7 | 22.66 | 27.61 | 32.63 | 41.74 |
| F44 | NA | NA | NA | 60.88 | 60.78 | NA | NA | NA |
| F46 | 32.05 | 32.23 | 32.01 | 44.12 | 44.17 | 43.92 | 43.66 | 44.19 |
| F47 | 35.06 | 35.08 | 34.76 | 71.96 | 72.05 | 71.83 | 70.73 | 66.98 |
| F48 | 23.93 | NA | NA | 50.33 | 50.32 | 50.12 | NA | NA |
| F49 | 28.27 | 28.23 | 28.05 | 53.48 | 53.29 | 52.22 | 49.71 | 43.93 |
| F50 | 30.12 | 30.2 | 30.23 | 48.6 | 47.39 | 50.33 | 53.51 | 54.52 |
| F51 | 36.06 | 36.02 | 35.87 | 79.53 | 78.61 | 74.81 | 69.2 | 58.45 |
| F52 | 35.24 | 35.39 | 35.36 | 34.78 | 34.5 | 34.7 | 36.38 | 40.46 |
| F53 | 43.32 | 43.64 | 43.08 | 31.99 | 32.41 | 33.83 | 36.64 | 41.61 |
| F54 | 41.44 | 41.08 | 40.72 | 26.4 | 26.84 | 28.94 | 31.5 | 32.44 |
| F55 | 31.8 | 31.71 | NA | 35.44 | 35.58 | 36.02 | 35.8 | NA |
| F56 | 21.91 | 22.52 | 23.21 | 34.83 | 34.85 | 35.03 | 35.07 | 34.95 |

| ID | CORINE (r = 300 m) | CORINE (r = 500 m) | CORINE (r = 1000 m) | CORINE (r = 1500 m) | CORINE (r = 2000 m) | CORINE (r = 3000 m) | CORINE (r = 4000 m) | CORINE (r = 5000 m) |
|---|---|---|---|---|---|---|---|---|
| F02 | 0.2241 | 0.2154 | 0.1804 | 0.1852 | 0.1561 | 0.1442 | 0.1604 | 0.1506 |
| F06 | 0.1199 | 0.2263 | 0.2327 | 0.172 | 0.1397 | 0.1258 | 0.1389 | 0.1466 |
| F08 | 0.0744 | 0.0787 | 0.0553 | 0.066 | 0.1031 | 0.1241 | 0.1273 | 0.1347 |
| F09 | 0.0687 | 0.0363 | 0.0418 | 0.0662 | 0.0702 | 0.0868 | 0.0998 | 0.1158 |
| F11 | 0.052 | 0.093 | 0.0964 | 0.0807 | 0.0786 | 0.0845 | 0.0956 | 0.1072 |
| F12 | 0.0618 | 0.0741 | 0.0945 | 0.0893 | 0.0814 | 0.0874 | 0.0873 | 0.0994 |
| F13 | 0.0096 | 0.0173 | 0.044 | 0.0488 | 0.0636 | 0.1063 | 0.1382 | 0.1358 |
| F14 | 0.0779 | 0.0685 | 0.0423 | 0.038 | 0.0557 | 0.0948 | 0.1334 | 0.1333 |
| F16 | 0.1181 | 0.1023 | 0.0665 | 0.0742 | 0.0872 | 0.1087 | 0.1283 | 0.1506 |
| F18 | 0.0749 | 0.0369 | 0.0385 | 0.0507 | 0.0478 | 0.0923 | 0.1283 | 0.1393 |
| F19 | 0.0828 | 0.0922 | 0.0568 | 0.0673 | 0.0741 | 0.0977 | 0.1309 | 0.1515 |
| F21 | 0.2045 | 0.1555 | 0.08 | 0.0812 | 0.0878 | 0.1033 | 0.1418 | 0.1543 |
| F22 | 0.0765 | 0.1025 | 0.079 | 0.0713 | 0.0706 | 0.094 | 0.1398 | 0.1528 |
| F23 | 0.2131 | 0.1482 | 0.094 | 0.0832 | 0.0874 | 0.1048 | 0.1445 | 0.1563 |
| F24 | 0.0407 | 0.0327 | 0.0306 | 0.0443 | 0.0585 | 0.068 | 0.0753 | 0.0742 |
| F25 | 0.1016 | 0.1075 | 0.1051 | 0.0854 | 0.0944 | 0.0973 | 0.0829 | 0.0764 |
| F26 | 0.0811 | 0.0843 | 0.106 | 0.089 | 0.0918 | 0.0971 | 0.0809 | 0.0756 |
| F27 | 0.0169 | 0.0123 | 0.0548 | 0.0945 | 0.0973 | 0.0885 | 0.0824 | 0.0738 |
| F28 | 0.1275 | 0.0808 | 0.0674 | 0.0628 | 0.08 | 0.0923 | 0.0769 | 0.0757 |
| F29 | 0.0694 | 0.0669 | 0.0919 | 0.0661 | 0.0691 | 0.071 | 0.0822 | 0.08 |
| F30 | 0.0272 | 0.0184 | 0.0436 | 0.0426 | 0.053 | 0.0596 | 0.0629 | 0.0643 |
| F31 | 0.0308 | 0.0298 | 0.0459 | 0.0622 | 0.0658 | 0.0612 | 0.0584 | 0.0656 |
| F33 | 0.0593 | 0.0717 | 0.0714 | 0.0636 | 0.0532 | 0.05 | 0.0528 | 0.0562 |
| F34 | 0.0046 | 0.009 | 0.0119 | 0.0249 | 0.0435 | 0.0641 | 0.0684 | 0.0655 |
| F35 | 0.0298 | 0.0255 | 0.0371 | 0.0409 | 0.0494 | 0.0707 | 0.0712 | 0.0727 |
| F36 | 0.1052 | 0.1081 | 0.097 | 0.0776 | 0.0575 | 0.0554 | 0.0651 | 0.0719 |
| F37 | 0.0527 | 0.0936 | 0.0621 | 0.0772 | 0.0976 | 0.109 | 0.0981 | 0.0853 |
| F39 | 0.0223 | 0.0246 | 0.0226 | 0.0357 | 0.0471 | 0.0688 | 0.0743 | 0.0792 |
| F40 | 0.0035 | 0.0464 | 0.0381 | 0.0341 | 0.0456 | 0.0618 | 0.0685 | 0.0738 |
| F41 | 0.086 | 0.0663 | 0.0713 | 0.0701 | 0.0656 | 0.063 | 0.0676 | 0.0783 |
| F42 | 0.0453 | 0.0694 | 0.1139 | 0.1057 | 0.1222 | 0.1197 | 0.1097 | 0.1077 |
| F44 | 0.0667 | 0.0911 | 0.0699 | 0.0747 | 0.0643 | 0.073 | 0.1026 | 0.106 |
| F46 | 0.0265 | 0.0564 | 0.1603 | 0.2007 | 0.1794 | 0.1399 | 0.1181 | 0.109 |
| F47 | 0.0348 | 0.0778 | 0.1246 | 0.144 | 0.1536 | 0.1339 | 0.1123 | 0.1053 |
| F48 | 0.3992 | 0.244 | 0.2139 | 0.2127 | 0.1788 | 0.139 | 0.1215 | 0.1123 |
| F49 | 0.223 | 0.1666 | 0.0937 | 0.0859 | 0.0945 | 0.0965 | 0.0902 | 0.0812 |
| F50 | 0.3458 | 0.251 | 0.1277 | 0.1164 | 0.1151 | 0.1046 | 0.0979 | 0.0854 |
| F51 | 0.0422 | 0.0176 | 0.0374 | 0.0519 | 0.0644 | 0.075 | 0.085 | 0.0923 |
| F52 | 0.0662 | 0.0503 | 0.0355 | 0.0522 | 0.0659 | 0.0728 | 0.0786 | 0.0876 |
| F53 | 0.0552 | 0.0481 | 0.0978 | 0.0781 | 0.0763 | 0.0766 | 0.0848 | 0.088 |
| F54 | 0.0308 | 0.0372 | 0.0592 | 0.062 | 0.0805 | 0.0831 | 0.0838 | 0.0836 |
| F55 | NA | NA | NA | NA | NA | NA | NA | NA |
| F56 | 0.0194 | 0.022 | 0.06 | 0.076 | 0.0702 | 0.0914 | 0.0854 | 0.0839 |

**Table A3. Species richness of saproxylic beetles and threatened saproxylic beetles in the tree hollows, and parameters of the examined tree hollows, hollow trees and surrounding forest structure at different spatial scales in the Kelheim study region.** SR = species richness of saproxylic beetles, RL = species richness of threatened saproxylic beetles. Parameters of tree hollows: H.a.s.l. = height above sea level, Volume = hollow volume, Entrance = size of the entrance, Height = height above ground, Decomp. = stage of decomposition, Temp. = temperature inside the hollows. Parameters of hollow trees: DBH = diameter at breast height. Parameters of surrounding forest structure: Hollows = number of tree hollows, Structures = number of microhabitat structures, DW (FI) = dead wood volume, DBH (FI) = average diameter at breast height of deciduous trees, CORINE = habitat proportion.

| ID | Latitude | Longitude | SR | RL | H.a.s.l. [m] | Volume [cm³] | Entrance [cm²] | Height [cm] | Decomp. | Temp. [°C] | DBH [cm] | Hollows (r = 30 m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| K02 | 48.89574 | 12.12136 | 6 | 1 | 426 | 16983 | 1232 | 130 | 2 | 16.92 | 75 | 1 |
| K07 | 48.9645 | 11.91799 | 6 | 2 | 481 | 180000 | 500 | 50 | 1 | 16.73 | 60 | 0 |
| K10 | 48.90694 | 11.85456 | 11 | 3 | 446 | 34560 | 700 | 113 | 1 | 17.8 | 30 | 4 |
| K11 | 48.98994 | 11.86334 | 6 | 0 | 511 | 2940 | 455 | 54 | 3 | 16.42 | 40 | 1 |
| K12 | 48.99363 | 11.86203 | 21 | 2 | 446 | 300000 | 17500 | 30 | 2 | 15.42 | 62 | 0 |
| K13 | 49.00356 | 11.82938 | 6 | 2 | 553 | 50400 | 3700 | 30 | 3 | 16.87 | 70 | 1 |
| K14 | 48.90404 | 11.85021 | 11 | 3 | 433 | 64800 | 1600 | 135 | 3 | 19.35 | 50 | 2 |
| K15 | 48.91082 | 11.80776 | 3 | 1 | 531 | 96800 | 1595 | 32 | 1 | 17.45 | 55 | 2 |
| K16 | 48.9153 | 11.81871 | 7 | 3 | 412 | 12000 | 200 | 80 | 3 | 17.43 | 50 | 1 |
| K17 | 48.91526 | 11.79754 | 6 | 0 | 477 | 27000 | 950 | 28 | 2 | 16.57 | 50 | 0 |
| K19 | 48.90431 | 11.96766 | 12 | 1 | 430 | 2340 | 112 | 16 | 3 | 16.25 | 28 | 0 |
| K20 | 48.92086 | 11.84294 | 6 | 2 | 427 | 51000 | 750 | 340 | 3 | 17.09 | 60 | 2 |
| K24 | 48.92098 | 11.83337 | 6 | 1 | 450 | 87040 | 4800 | 90 | 3 | 16.01 | 50 | 2 |
| K26 | 48.90964 | 11.82543 | 6 | 0 | 450 | 30800 | 2035 | 236 | 3 | 16.9 | 28 | 1 |
| K27 | 48.90113 | 11.82384 | 6 | 2 | 421 | 196020 | 2400 | 25 | 3 | 16.88 | 70 | 1 |
| K28 | 49.10983 | 11.51798 | 2 | 0 | 511 | 14400 | 90 | 45 | 2 | 14.55 | 90 | 2 |
| K32 | 48.93641 | 11.84531 | 2 | 0 | 470 | 12800 | 152 | 280 | 2 | 16.77 | 58 | 1 |
| K33 | 48.96608 | 11.88614 | 6 | 2 | 467 | 120000 | 7000 | 135 | 3 | 16.85 | 45 | 1 |
| K35 | 48.98581 | 11.90299 | 7 | 2 | 527 | 22500 | 1150 | 210 | 3 | 16.07 | 60 | 3 |
| K36 | 48.98311 | 11.8954 | 14 | 4 | 487 | 87500 | 880 | 35 | 2 | 16.2 | 80 | 0 |
| K37 | 48.97662 | 11.88419 | 12 | 4 | 494 | 300000 | 9400 | 0 | 1 | 16.12 | 70 | 1 |
| K38 | 49.09245 | 11.61628 | 9 | 2 | 551 | 23100 | 1100 | 0 | 2 | 18 | 63 | 1 |
| K41 | 49.12006 | 11.3638 | 5 | 0 | 520 | 112500 | 798 | 38 | 2 | 16.23 | 60 | 0 |
| K42 | 49.11681 | 11.40973 | 12 | 2 | 511 | 56000 | 2800 | 300 | 2 | 16.87 | 60 | 4 |
| K44 | 48.8874 | 11.74761 | 5 | 4 | 396 | 138000 | 2240 | 175 | 3 | 16.58 | 65 | 0 |
| K45 | 48.89753 | 11.75705 | 9 | 2 | 432 | 34560 | 600 | 0 | 2 | 17.15 | 40 | 3 |
| K46 | 48.90574 | 11.76873 | 3 | 0 | 435 | 8000 | 380 | 175 | 4 | 17.18 | 75 | 0 |
| K48 | 48.93118 | 11.76648 | 6 | 1 | 410 | 92000 | 2100 | 60 | 2 | 16.02 | 60 | 0 |
| K51 | 48.93661 | 11.74676 | 6 | 2 | 472 | 37050 | 1470 | 0 | 2 | 17.13 | 40 | 0 |
| K52 | 48.92968 | 11.73373 | 9 | 1 | 468 | 4320 | 245 | 185 | 3 | 16.51 | 30 | 0 |
| K58 | 49.05387 | 11.4324 | 5 | 0 | 470 | 14400 | 60 | 152 | 4 | 17.47 | 33 | 3 |
| K61 | 49.06728 | 11.45107 | 10 | 3 | 491 | 30000 | 400 | 150 | 3 | 18.05 | 36 | 6 |
| K67 | 49.15917 | 11.70044 | 9 | 5 | 566 | 74520 | 1120 | 135 | 3 | 19.45 | 40 | 0 |
| K68 | 48.90582 | 11.73757 | 10 | 2 | 493 | 90000 | 4800 | 100 | 2 | 17 | 65 | 1 |
| K69 | 48.90862 | 11.73008 | 12 | 2 | 475 | 18720 | 136 | 30 | 4 | 16.39 | 22 | 2 |
| K70 | 48.91435 | 11.74275 | 12 | 3 | 455 | 48620 | 3234 | 0 | 1 | 16.83 | 30 | 0 |
| K71 | 48.92756 | 11.74367 | 12 | 2 | 457 | 9000 | 100 | 60 | 3 | 15.3 | 75 | 0 |
| K72 | 49.03402 | 11.43063 | 6 | 0 | 500 | 1440 | 96 | 340 | 4 | 17.75 | 35 | 0 |
| K73 | 49.02455 | 11.4249 | 4 | 1 | 529 | 5850 | 432 | 320 | 3 | 17.41 | 50 | 0 |
| K74 | 48.96141 | 11.89253 | 7 | 0 | 517 | 32300 | 600 | 0 | 2 | 17.08 | 90 | 0 |
| K75 | 48.9027 | 11.7552 | 11 | 1 | 482 | 39375 | 1375 | 0 | 3 | 16.51 | 40 | 1 |

| ID | Structures (r = 30 m) | DW (FI) (r = 50 m) [m$^3$/ha] | DW (FI) (r = 100 m) [m$^3$/ha] | DW (FI) (r = 200 m) [m$^3$/ha] | DW (FI) (r = 300 m) [m$^3$/ha] | DBH (FI) (r = 50 m) [cm] | DBH (FI) (r = 100 m) [cm] | DBH (FI) (r = 200 m) [cm] |
|---|---|---|---|---|---|---|---|---|
| K02 | 11 | 17.36 | 16.47 | 15.42 | 14.46 | 48.08 | 46.69 | 44.28 |
| K07 | 3 | 82.4 | 72.48 | 50.38 | 41.01 | 40.13 | 39.87 | 39.97 |
| K10 | 12 | 63.94 | 56.4 | 45.72 | 42.16 | 39.39 | 39.27 | 39.73 |
| K11 | 5 | 15.85 | 15.79 | 15.55 | 15.16 | 39.45 | 39.26 | 38.43 |
| K12 | 2 | 16.72 | 16.74 | 16.65 | 16.33 | 33.78 | 33.82 | 34.22 |
| K13 | 5 | 58.61 | 59.36 | 60.91 | 60.51 | 38.33 | 38.16 | 37.18 |
| K14 | 22 | 55.01 | 73.02 | 84.25 | 75.04 | 49.19 | 49.13 | 47.25 |
| K15 | 5 | 29.35 | 30.01 | 32.96 | 35.94 | 19.6 | 24.63 | 30.09 |
| K16 | 2 | 17.16 | 16.37 | 15.73 | 16.74 | 38.14 | 38.22 | 38.65 |
| K17 | 3 | 11.45 | 11.52 | 12.34 | 13.01 | 33.8 | 33.91 | 32.27 |
| K19 | 3 | 16.08 | 16.08 | 16.05 | 15.79 | 49.02 | 47.66 | 42.98 |
| K20 | 6 | 17.93 | 17.84 | 17.74 | 18.30 | 37.56 | 35.05 | 32.23 |
| K24 | 6 | 25.04 | 25.21 | 26.56 | 28.35 | 37.71 | 37.73 | 38.05 |
| K26 | 5 | 21.24 | 21.75 | 23.53 | 27.01 | 41.37 | 41.58 | 42.3 |
| K27 | 9 | 25.67 | 30.55 | 43.85 | 43.53 | 29.72 | 31.48 | 34.8 |
| K28 | 6 | 22.96 | 23.23 | 23.80 | 24.75 | 32.58 | 33.4 | 35.46 |
| K32 | 4 | 31.47 | 31.42 | 31.46 | 30.66 | 25.03 | 24.93 | 26.25 |
| K33 | 7 | 28.83 | 28.23 | 27.15 | 28.34 | 39.45 | 39.34 | 37.89 |
| K35 | 13 | 10.68 | 10.67 | 10.86 | 11.02 | 29.35 | 28.97 | 28.58 |
| K36 | 1 | 14.75 | 14.9 | 14.82 | 14.41 | 22.4 | 22.35 | 22.31 |
| K37 | 2 | 14.17 | 14.33 | 15.10 | 17.9 | 33.19 | 33.13 | 33.03 |
| K38 | 3 | 24.78 | 25.1 | 25.25 | 24.56 | 36.61 | 36.48 | 34.52 |
| K41 | 5 | 7.17 | 7.23 | 7.46 | 7.67 | 52.53 | 52.64 | 52.23 |
| K42 | 7 | 15.88 | 15.80 | 15.50 | 15.29 | 40.38 | 40.38 | 42.3 |
| K44 | 2 | 21.09 | 21.11 | 20.82 | 20.66 | 35.6 | 35.69 | 35.99 |
| K45 | 4 | 25.67 | 25.88 | 27.07 | 28.99 | 28.96 | 28.58 | 27.97 |
| K46 | 3 | 14.35 | 15.13 | 16.53 | 18.47 | 27.69 | 27.86 | 28.96 |
| K48 | 4 | 16.05 | 18.57 | 20.50 | 19.91 | 38.42 | 39.89 | 43.84 |
| K51 | 4 | 17.65 | 18.14 | 19.77 | 21.82 | 32.7 | 32.83 | 33.42 |
| K52 | 5 | 15.06 | 15.02 | 14.95 | 15.05 | 33.19 | 33.15 | 33.29 |
| K58 | 8 | 22.5 | 22.24 | 22.66 | 25 | 47.36 | 40.79 | 35.98 |
| K61 | 13 | 23.84 | 25.98 | 28.64 | 26.75 | 47.66 | 45.48 | 40.34 |
| K67 | 5 | 19.74 | 19.78 | 19.96 | 20.59 | 50.82 | 51.05 | 50.98 |
| K68 | 12 | 19.43 | 19.5 | 20.12 | 20.91 | 39.85 | 40.18 | 42.03 |
| K69 | 6 | 24.84 | 25.02 | 26.35 | 27.17 | 38.88 | 38.81 | 38.7 |
| K70 | 1 | 19.32 | 19.55 | 21.03 | 24.32 | 40.64 | 40.99 | 40.56 |
| K71 | 1 | 27.84 | 27.86 | 28.12 | 27.65 | 43.56 | 44.09 | 43.27 |
| K72 | 2 | 9.98 | 9.88 | 9.76 | 9.78 | 35.89 | 36.14 | 36.08 |
| K73 | 4 | 13.25 | 12.96 | 11.57 | 10.01 | 43.55 | 43.61 | 43.2 |
| K74 | 1 | 36.43 | 36.61 | 37.28 | 37.77 | 30.42 | 31.11 | 34.06 |
| K75 | 4 | 21.28 | 20.85 | 20.40 | 22.03 | 44.16 | 44.48 | 44.17 |

| ID | DBH (FI) (r = 300 m) [cm] | CORINE (r = 300 m) | CORINE (r = 500 m) | CORINE (r = 1000 m) | CORINE (r = 1500 m) | CORINE (r = 2000 m) | CORINE (r = 3000 m) | CORINE (r = 4000 m) | CORINE (r = 5000 m) |
|---|---|---|---|---|---|---|---|---|---|
| K02 | 42.46 | 0.4857 | 0.3954 | 0.2291 | 0.1895 | 0.1396 | 0.0964 | 0.1004 | 0.1 |
| K07 | 39.87 | 0.5791 | 0.5465 | 0.4398 | 0.3873 | 0.3842 | 0.3191 | 0.259 | 0.233 |
| K10 | 40.43 | 0.7872 | 0.7562 | 0.7027 | 0.6432 | 0.5724 | 0.445 | 0.3691 | 0.3242 |
| K11 | 36.3 | 0.5385 | 0.3508 | 0.1964 | 0.2018 | 0.1959 | 0.2058 | 0.1911 | 0.1889 |
| K12 | 34.32 | 0.2383 | 0.2633 | 0.2504 | 0.2033 | 0.1974 | 0.1968 | 0.1773 | 0.1769 |
| K13 | 35.22 | 0.7023 | 0.4538 | 0.2735 | 0.192 | 0.1586 | 0.1327 | 0.1098 | 0.103 |
| K14 | 45.73 | 0.7499 | 0.721 | 0.7391 | 0.6815 | 0.6064 | 0.4532 | 0.3635 | 0.3203 |
| K15 | 32.76 | 0.971 | 0.9116 | 0.8094 | 0.7222 | 0.6321 | 0.535 | 0.495 | 0.4313 |
| K16 | 39.18 | 0.755 | 0.7136 | 0.8179 | 0.7536 | 0.6897 | 0.6033 | 0.4858 | 0.4217 |
| K17 | 31.06 | 0.6576 | 0.6759 | 0.7813 | 0.6649 | 0.5719 | 0.5418 | 0.5179 | 0.4565 |
| K19 | 40.11 | 0.7498 | 0.595 | 0.3597 | 0.2385 | 0.1764 | 0.154 | 0.1379 | 0.12 |
| K20 | 31.73 | 0.7659 | 0.5854 | 0.6116 | 0.6195 | 0.5818 | 0.5266 | 0.4702 | 0.3961 |
| K24 | 38.88 | 0.7323 | 0.6534 | 0.5844 | 0.6596 | 0.671 | 0.5765 | 0.4784 | 0.406 |
| K26 | 42.54 | 0.9742 | 0.913 | 0.8569 | 0.7714 | 0.6866 | 0.5712 | 0.4567 | 0.3884 |
| K27 | 36.15 | 0.8107 | 0.6962 | 0.6866 | 0.6055 | 0.5779 | 0.4868 | 0.4193 | 0.3614 |
| K28 | 37.17 | 0.6903 | 0.5977 | 0.4187 | 0.2748 | 0.1881 | 0.1134 | 0.0919 | 0.0954 |
| K32 | 28.25 | 0.6154 | 0.5588 | 0.5033 | 0.3723 | 0.4063 | 0.3997 | 0.41 | 0.4111 |
| K33 | 36.1 | 0.4308 | 0.5797 | 0.5327 | 0.4463 | 0.396 | 0.3301 | 0.2913 | 0.2596 |
| K35 | 29.17 | 0.2197 | 0.2575 | 0.267 | 0.237 | 0.2199 | 0.2507 | 0.2412 | 0.2322 |
| K36 | 22.33 | 0.2354 | 0.3459 | 0.3303 | 0.3068 | 0.2586 | 0.2595 | 0.2435 | 0.2362 |
| K37 | 34.01 | 0.2549 | 0.331 | 0.3679 | 0.3752 | 0.3394 | 0.2681 | 0.2594 | 0.2466 |
| K38 | 33.42 | 0.8619 | 0.7994 | 0.4844 | 0.3785 | 0.2839 | 0.1885 | 0.1402 | 0.1382 |
| K41 | 50.79 | 0.7613 | 0.663 | 0.4092 | 0.2491 | 0.1709 | 0.1221 | 0.123 | 0.1215 |
| K42 | 43.2 | 0.8593 | 0.5643 | 0.2997 | 0.2607 | 0.2069 | 0.1772 | 0.1699 | 0.149 |
| K44 | 35.53 | 0.5339 | 0.344 | 0.3464 | 0.3341 | 0.2898 | 0.2199 | 0.1986 | 0.2117 |
| K45 | 29.07 | 0.9402 | 0.8188 | 0.6191 | 0.4886 | 0.401 | 0.3164 | 0.3015 | 0.2852 |
| K46 | 30.11 | 0.4095 | 0.4385 | 0.3907 | 0.3919 | 0.414 | 0.4651 | 0.4023 | 0.3652 |
| K48 | 44.15 | 0.8746 | 0.8511 | 0.7626 | 0.6287 | 0.5648 | 0.468 | 0.4308 | 0.3928 |
| K51 | 34.9 | 0.3953 | 0.4754 | 0.4587 | 0.5463 | 0.5251 | 0.4048 | 0.3441 | 0.3419 |
| K52 | 32.9 | 0.6066 | 0.4628 | 0.4058 | 0.413 | 0.377 | 0.3449 | 0.3568 | 0.3358 |
| K58 | 36.61 | 0.7124 | 0.5839 | 0.3983 | 0.3269 | 0.3101 | 0.2501 | 0.211 | 0.1896 |
| K61 | 37.27 | 0.7131 | 0.5352 | 0.3607 | 0.3058 | 0.3042 | 0.2292 | 0.1824 | 0.1589 |
| K67 | 47.73 | 0.9568 | 0.7609 | 0.3641 | 0.2775 | 0.2865 | 0.2813 | 0.2277 | 0.2038 |
| K68 | 43.34 | 0.5179 | 0.423 | 0.3523 | 0.3601 | 0.3465 | 0.3048 | 0.2936 | 0.2952 |
| K69 | 39.19 | 0.186 | 0.2257 | 0.2723 | 0.2705 | 0.2869 | 0.2962 | 0.2949 | 0.2881 |
| K70 | 39.72 | 0.0768 | 0.269 | 0.3831 | 0.3518 | 0.3754 | 0.3813 | 0.365 | 0.3354 |
| K71 | 40.22 | 0.5529 | 0.629 | 0.5551 | 0.5197 | 0.4658 | 0.3827 | 0.3813 | 0.3577 |
| K72 | 36.38 | 0.1678 | 0.1863 | 0.3889 | 0.3907 | 0.3004 | 0.229 | 0.2215 | 0.2148 |
| K73 | 42.3 | 0.618 | 0.5995 | 0.4338 | 0.3323 | 0.2928 | 0.198 | 0.2263 | 0.2371 |
| K74 | 36.15 | 0.9151 | 0.8235 | 0.5537 | 0.4929 | 0.4475 | 0.3664 | 0.2903 | 0.2542 |
| K75 | 43.03 | 0.8084 | 0.6275 | 0.4532 | 0.4627 | 0.4237 | 0.3626 | 0.3387 | 0.3108 |

**Table A4. List of saproxylic beetle species and number of individuals found in the tree hollows in the three study regions.** Red List status of saproxylic beetle species according to the Red List of Germany (2021), the Red List of Bavaria (2005) and the Red List of Germany (1998). Ecological status as tree hollow specialist species according to Heinz Bussler (personal communication). 0 = extinct or lost, 1 = threatened with extinction, 2 = highly threatened, 3 = threatened, UE = threat of unknown extent, NT = near threatened, DD = data deficient.

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Abraeus perpusillus* | Histeridae | 10-.005-.003-. | 17 | | 2 | | | | |
| *Acalles roboris* | Curculionidae | 93-.135-.002-. | 1 | | | | | | |
| *Acrotrichis brevipennis* | Ptiliidae | 21-.019-.007-. | 15 | | | | | | |
| *Acrotrichis montandonii* | Ptiliidae | 21-.019-.002-. | 10 | | | | | | |
| *Agathidium seminulum* | Leiodidae | 16-.011-.015-. | 1 | | | | | | |
| *Aleochara sanguinea* | Staphylinidae | 23-.237-.026-. | | | 1 | | | | |
| *Aleochara sparsa* | Staphylinidae | 23-.237-.015-. | 135 | 37 | 382 | | | | |
| *Aleochara stichai* | Staphylinidae | 23-.237-.016-. | 19 | | 4 | | | | |
| *Allecula morio* | Tenebrionidae | 82-.001-.002-. | 4 | | | 3 | 3 | 3 | yes |
| *Allecula rhenana* | Tenebrionidae | 82-.001-.003-. | 7 | | 4 | 2 | | 2 | yes |
| *Alosterna tabacicolor* | Cerambycidae | 87-.024-.001-. | 4 | | 12 | | | | |
| *Ampedus brunnicornis* | Elateridae | 34-.001-.013-. | 1 | | | 1 | 1 | 1 | |
| *Ampedus balteatus* | Elateridae | 34-.001-.008-. | 1 | | 1 | | | | |
| *Ampedus erythrogonus* | Elateridae | 34-.001-.004-. | 1 | 1 | | 3 | 3 | 3 | |
| *Ampedus pomorum* | Elateridae | 34-.001-.019-. | 6 | | 4 | | | | |
| *Anaglyptus mysticus* | Cerambycidae | 87-.063-.001-. | 10 | 1 | | | | | |
| *Anaspis flava* | Scraptiidae | 73-.004-.022-. | 1 | | 2 | | | | |
| *Anaspis frontalis* | Scraptiidae | 73-.004-.009-. | 1 | | | | | | |
| *Anaspis marginicollis* | Scraptiidae | 73-.004-.011-. | 10 | 6 | 5 | | 2 | DD | |
| *Anaspis ruficollis* | Scraptiidae | 73-.004-.013-. | 9 | 19 | 4 | 2 | 2 | | |
| *Anaspis rufilabris* | Scraptiidae | 73-.004-.019-. | 1 | | 9 | | | | |
| *Anaspis thoracica* | Scraptiidae | 73-.004-.012-. | 5 | | 1 | | | | |
| *Anisarthron barbipes* | Cerambycidae | 87-.047-.001-. | 1 | | | 2 | | 3 | |
| *Anisotoma castanea* | Leiodidae | 16-.007-.003-. | 1 | | | | | | |
| *Anisotoma humeralis* | Leiodidae | 16-.007-.001-. | 1 | 1 | 1 | | | | |
| *Anisotoma orbicularis* | Leiodidae | 16-.007-.005-. | 1 | | | | | | |
| *Anisoxya fuscula* | Melandryidae | 80-.006-.001-. | | | 1 | 3 | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Anobium nitidum* | Anobiidae | 68-.012-.004-. | 3 | | | | | | |
| *Anthobium atrocephalum* | Staphylinidae | 23-.025-.002-. | 1 | | | | | | |
| *Anthophagus angusticollis* | Staphylinidae | 23-.035-.013-. | | 4 | | | | | |
| *Anthribus albinus* | Anthribidae | 90-.010-.001-. | 2 | 1 | 1 | | | | |
| *Apocatops nigritus* | Leiodidae | 14-.0111.001-. | 1 | | | | | | |
| *Arpidiphorus orbiculatus* | Sphindidae | 63-.002-.001-. | 14 | | | | | | |
| *Arthrolips obscurus* | Corylophidae | 601.002-.001-. | | | 2 | 2 | | DD | |
| *Atheta britanniae* | Staphylinidae | 23-.188-.198-. | 7 | | 1 | | | | |
| *Atheta coriaria* | Staphylinidae | 23-.188-.181-. | | 1 | | | | | |
| *Atheta fungi* | Staphylinidae | 23-.188-.136-. | | 1 | | | | | |
| *Atheta nigricornis* | Staphylinidae | 23-.188-.045-. | 9 | 26 | 11 | | | | |
| *Atheta pallidicornis* | Staphylinidae | 23-.188-.111-. | 7 | | | | | | |
| *Atheta picipes* | Staphylinidae | 23-.188-.126-. | 1 | | | | | | |
| *Atheta sodalis* | Staphylinidae | 23-.188-.109-. | 2 | 5 | | | | | |
| *Athous subfuscus* | Elateridae | 34-.041-.003-. | 4 | 1 | 1 | | | | |
| *Atomaria nigrirostris* | Cryptophagidae | 55-.014-.045-. | 1 | | | | | | |
| *Aulonothroscus brevicollis* | Throscidae | 37-.002-.001-. | 2 | | 2 | | | | |
| *Barypeithes pellucidus* | Curculionidae | 93-.037-.011-. | 2 | | | | | | |
| *Barypeithes tenex* | Curculionidae | 93-.037-.002-. | | | 3 | | | | |
| *Batrisodes delaporti* | Staphylinidae | 24-.015-.001-. | 2 | | | | | | |
| *Batrisus formicarius* | Staphylinidae | 24-.014-.001-. | 1 | | | | | NT | |
| *Bibloporus minutus* | Staphylinidae | 24-.002-.003-. | 1 | | | | | | |
| *Bolitobius inclinans* | Staphylinidae | 23-.112-.003-. | | 1 | | | | | |
| *Bolitochara obliqua* | Staphylinidae | 23-.147-.001-. | 5 | | | | | | |
| *Brachysomus echinatus* | Curculionidae | 93-.035-.006-. | 1 | | | | | | |
| *Brachytarsus nebulosus* | Anthribidae | 90-.012-.003-. | | 7 | | | | | |
| *Bryaxis puncticollis* | Staphylinidae | 24-.018-.008-. | 1 | | | | | | |
| *Cantharis decipiens* | Cantharidae | 27-.002-.025-. | 3 | | | | | | |
| *Cartodere nodifer* | Latridiidae | 58-.005-.0031. | | 1 | | | | | |
| *Catops neglectus* | Leiodidae | 14-.011-.010-. | 1 | | | | | | |
| *Catops picipes* | Leiodidae | 14-.011-.020-. | 1 | | | | | | |
| *Catops tristis* | Leiodidae | 14-.011-.007-. | | 1 | | | | | |
| *Cephennium thoracicum* | Scydmaenidae | 18-.004-.003-. | 1 | | | | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Cerophytum elateroides* | Cerophytidae | 35-.001-.001-. | 12 | | | 2 | 2 | 2 | |
| *Cerylon fagi* | Cerylonidae | 492.002-.001-. | 2 | | | | | | |
| *Cerylon ferrugineum* | Cerylonidae | 492.002-.003-. | | 1 | | | | | |
| *Cerylon histeroides* | Cerylonidae | 492.002-.002-. | 1 | | 1 | | | | |
| *Cicones variegatus* | Colydiidae | 60-.014-.001-. | 2 | | | 3 | | | |
| *Cis boleti* | Ciidae | 65-.006-.011-. | 2 | | | | | | |
| *Cis dentatus* | Ciidae | 65-.006-.016-. | | 1 | | 3 | | | |
| *Cis fusciclavis* | Ciidae | 65-.006-.015-. | 1 | | | | | | |
| *Cis glabratus* | Ciidae | 65-.006-.004-. | 1 | | | 3 | | | |
| *Cis nitidus* | Ciidae | 65-.006-.002-. | 5 | | | | | | |
| *Clambus punctulum* | Clambidae | 381.002-.002-. | 1 | 15 | | | | | |
| *Clytus arietis* | Cerambycidae | 87-.058-.003-. | 1 | | | | | | |
| *Corticaria alleni* | Latridiidae | 58-.007-.0172. | 1 | | | 2 | | DD | |
| *Corticaria longicollis* | Latridiidae | 58-.007-.018-. | | | 2 | | | | |
| *Corticarina obfuscata* | Latridiidae | 58-.008-.003-. | 1 | | 1 | 2 | 2 | DD | |
| *Cortinicara gibbosa* | Latridiidae | 58-.0081.001-. | | 1 | | | | | |
| *Corymbia scutellata* | Cerambycidae | 87-.0274.009-. | 2 | | 2 | | 2 | 3 | |
| *Coryphium angusticolle* | Staphylinidae | 23-.037-.003-. | | 4 | | | | | |
| *Crataraea suturalis* | Staphylinidae | 23-.233-.001-. | 1 | | | | | | |
| *Crepidophorus mutilatus* | Elateridae | 34-.040-.001-. | 3 | | | 2 | 1 | 2 | yes |
| *Cryptolestes ferrugineus* | Laemophloeidae | 561.004-.005-. | 1 | | 1 | | | | |
| *Cryptolestes minutus* | Laemophloeidae | 561.004-.002-. | 1 | | | | | | |
| *Cryptophagus dentatus* | Cryptophagidae | 55-.008-.027-. | 11 | 11 | 2 | | | | |
| *Cryptophagus deubeli* | Cryptophagidae | 55-.008-.053-. | 1 | 8 | | 1 | 1 | | |
| *Cryptophagus labilis* | Cryptophagidae | 55-.008-.023-. | | 1 | | 2 | 2 | NT | yes |
| *Cryptophagus micaceus* | Cryptophagidae | 55-.008-.020-. | | | 14 | 2 | | | |
| *Cryptophagus pallidus* | Cryptophagidae | 55-.008-.035-. | 5 | | | | | | |
| *Cryptophagus pilosus* | Cryptophagidae | 55-.008-.042-. | 5 | | | | | | |
| *Cryptophagus scanicus* | Cryptophagidae | 55-.008-.034-. | 2 | | 4 | | | | |
| *Cryptophagus thomsoni* | Cryptophagidae | 55-.008-.037-. | 1 | | | | | | |
| *Dalopius marginatus* | Elateridae | 34-.009-.001-. | 2 | | | | | | |
| *Dasycerus sulcatus* | Staphylinidae | 23-.0061.001-. | 1 | | | | | | |
| *Dasytes cyaneus* | Dasytidae | 30-.005-.005-. | 1 | | | | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Denticollis linearis* | Elateridae | 34-.033-.004-. |  | 1 | 1 |  |  |  |  |
| *Dienerella clathrata* | Latridiidae | 58-.0041.0021. | 31 |  | 6 |  |  |  |  |
| *Dienerella elongata* | Latridiidae | 58-.0041.001-. |  | 32 | 7 |  |  |  |  |
| *Dinaraea linearis* | Staphylinidae | 23-.182-.003-. | 1 |  |  |  |  |  |  |
| *Diplocoelus fagi* | Biphyllidae | 541.002-.001-. | 5 |  |  |  |  |  |  |
| *Dorcatoma dresdensis* | Ptinidae | 68-.022-.006-. | 1 |  |  | 3 | 3 |  |  |
| *Dorcatoma substriata* | Ptinidae | 68-.022-.004-. | 30 |  |  | 2 | 2 | NT |  |
| *Dorcus parallelipipedus* | Lucanidae | 86-.002-.001-. | 3 |  |  |  |  |  |  |
| *Dryocoetes autographus* | Scolytidae | 91-.024-.001-. |  | 2 |  |  |  |  |  |
| *Dryocoetes villosus* | Scolytidae | 91-.024-.002-. | 1 |  |  |  |  |  |  |
| *Echinodera hypocrita* | Curculionidae | 93-.135-.017-. | 8 |  | 2 |  |  |  |  |
| *Enicmus brevicornis* | Latridiidae | 58-.004-.009-. | 36 |  |  | 3 |  |  |  |
| *Enicmus rugosus* | Latridiidae | 58-.004-.012-. | 2 |  |  |  |  |  |  |
| *Ennearthron cornutum* | Ciidae | 65-.007-.002-. | 1 |  |  |  |  |  |  |
| *Epuraea marseuli* | Nitidulidae | 50-.009-.015-. | 1 |  |  |  |  |  |  |
| *Epuraea neglecta* | Nitidulidae | 50-.009-.005-. |  |  | 2 |  |  |  |  |
| *Epuraea pygmaea* | Nitidulidae | 50-.009-.016-. |  | 2 | 1 |  |  |  |  |
| *Epuraea variegata* | Nitidulidae | 50-.009-.028-. |  | 1 | 1 |  |  |  |  |
| *Eucnemis capucina* | Eucnemidae | 36-.003-.001-. | 27 | 2 | 24 | 3 | 3 | 3 | yes |
| *Euconnus pragensis* | Scydmaenidae | 18-.009-.015-. |  |  | 2 | 3 |  | UE |  |
| *Euplectus karstenii* | Staphylinidae | 24-.006-.015-. | 9 |  |  |  |  |  |  |
| *Euplectus nanus* | Staphylinidae | 24-.006-.001-. | 1 |  | 2 |  |  |  |  |
| *Euplectus punctatus* | Staphylinidae | 24-.006-.013-. | 1 |  |  |  |  |  |  |
| *Eusphalerum limbatum* | Staphylinidae | 23-.010-.025-. |  | 1 |  |  |  |  |  |
| *Eusphalerum signatum* | Staphylinidae | 23-.010-.024-. |  | 1 |  |  |  |  |  |
| *Fissocatops westi* | Leiodidae | 14-.0112.015-. |  | 1 |  |  |  |  |  |
| *Glischrochilus hortensis* | Nitidulidae | 50-.021-.002-. | 1 |  |  |  |  |  |  |
| *Gnathoncus buyssoni* | Histeridae | 10-.009-.004-. | 2 | 3 | 1 |  |  |  |  |
| *Habrocerus capillaricornis* | Staphylinidae | 23-.107-.001-. | 1 |  |  |  |  |  |  |
| *Halyzia sedecimguttata* | Coccinellidae | 62-.035-.001-. | 1 |  |  | 3 |  |  |  |
| *Hapalaraea pygmaea* | Staphylinidae | 23-.0141.001-. | 15 |  | 5 | 3 | 3 |  |  |
| *Haploglossa gentilis* | Staphylinidae | 23-.234-.001-. | 1 |  |  | 3 |  | NT |  |
| *Haploglossa villosula* | Staphylinidae | 23-.234-.002-. | 5 | 6 | 9 |  |  |  |  |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Hedobia imperialis* | Anobiidae | 68-.001-.002-. | 1 | | | | | | |
| *Hesperus rufipennis* | Staphylinidae | 23-.087-.001-. | 22 | | | 2 | 0 | 2 | yes |
| *Holobus apicatus* | Staphylinidae | 23-.1261.002-. | 1 | | | 3 | 3 | | |
| *Homoeusa acuminata* | Staphylinidae | 23-.230-.001-. | 1 | | | | | | |
| *Hylastes cunicularius* | Scolytidae | 91-.004-.003-. | | 13 | | | | | |
| *Hylecoetus dermestoides* | Lymexylidae | 33-.001-.001-. | | 1 | | | | | |
| *Hypebaeus flavipes* | Malachiidae | 29-.003-.001-. | 7 | | 1 | 3 | 3 | 3 | |
| *Ischnomera caerulea* | Oedemeridae | 70-.007-.002-. | 5 | | | 3 | | UE | |
| *Ischnomera sanguinicollis* | Oedemeridae | 70-.007-.001-. | 17 | | | 3 | 2 | 3 | yes |
| *Lagria atripes* | Tenebrionidae | 81-.001-.002-. | 1 | | | | | | |
| *Lathrobium fulvipenne* | Staphylinidae | 23-.068-.021-. | | 1 | | | | | |
| *Leptura maculata* | Cerambycidae | 87-.027-.0041. | | 1 | | | | | |
| *Leptusa fumida* | Staphylinidae | 23-.141-.004-. | 3 | 2 | | | | | |
| *Leptusa ruficollis* | Staphylinidae | 23-.141-.006-. | 1 | | | | | | |
| *Litargus connexus* | Mycetophagidae | 59-.003-.001-. | 4 | | 3 | | | | |
| *Lordithon exoletus* | Staphylinidae | 23-.111-.005-. | 1 | 1 | | | | | |
| *Lordithon lunulatus* | Staphylinidae | 23-.111-.007-. | | | 1 | | | | |
| *Lordithon trinotatus* | Staphylinidae | 23-.111-.006-. | 3 | | | | | | |
| *Malachius bipustulatus* | Malachiidae | 29-.006-.0032. | 1 | | | | | | |
| *Malthinus frontalis* | Cantharidae | 27-.008-.010-. | | | 1 | | | | |
| *Malthinus punctatus* | Cantharidae | 27-.008-.001-. | 1 | 1 | | | | | |
| *Malthodes fuscus* | Cantharidae | 27-.009-.011-. | | | 2 | | | | |
| *Malthodes guttifer* | Cantharidae | 27-.009-.015-. | | 3 | 2 | | | | |
| *Malthodes marginatus* | Cantharidae | 27-.009-.016-. | 2 | 1 | 1 | | | | |
| *Malthodes pumilus* | Cantharidae | 27-.009-.022-. | 1 | | | | | | |
| *Margarinotus striola* | Histeridae | 10-.029-.008-. | 1 | | | | | | |
| *Medon fusculus* | Staphylinidae | 23-.062-.006-. | 1 | | | | | | |
| *Melanotus castanipes* | Elateridae | 34-.016-.003-. | 4 | 2 | 4 | | | | |
| *Melanotus rufipes* | Elateridae | 34-.016-.002-. | 21 | 8 | 4 | | | | |
| *Microscydmus minimus* | Scydmaenidae | 18-.008-.002-. | 48 | | 6 | 3 | | | |
| *Mniusa incrassata* | Staphylinidae | 23-.219-.001-. | | 2 | | | | | |
| *Mycetochara axillaris* | Tenebrionidae | 82-.008-.002-. | 1 | | 27 | 2 | 2 | 2 | yes |
| *Mycetochara linearis* | Tenebrionidae | 82-.008-.011-. | 2 | | 4 | | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Mycetophagus atomarius* | Mycetophagidae | 59-.004-.006-. | 2 | | | | | | |
| *Mycetophagus piceus* | Mycetophagidae | 59-.004-.003-. | 3 | | | 3 | 3 | NT | |
| *Mycetophagus populi* | Mycetophagidae | 59-.004-.010-. | 4 | | 2 | 2 | 2 | 3 | |
| *Mycetophagus quadriguttatus* | Mycetophagidae | 59-.004-.007-. | | | 1 | | | | |
| *Mycetophagus quadripustulatu* | Mycetophagidae | 59-.004-.001-. | 1 | | 2 | | | | |
| *Nalassus laevioctostriatus* | Tenebrionidae | 83-.041-.001-. | 17 | | | | | | |
| *Nemosoma elongatum* | Trogossitidae | 321.001-.001-. | 1 | | | | | | |
| *Neuraphes carinatus* | Scydmaenidae | 18-.005-.005-. | | | 4 | | | NT | |
| *Neuraphes elongatulus* | Scydmaenidae | 18-.005-.001-. | 1 | | | | | | |
| *Neuraphes plicicollis* | Scydmaenidae | 18-.005-.012-. | 1 | | | | | | |
| *Neuraphes praeteritus* | Scydmaenidae | 18-.005-.019-. | 1 | | | | | | |
| *Nicrophorus vespilloides* | Silphidae | 12-.001-.006-. | 2 | | | | | | |
| *Oligota granaria* | Staphylinidae | 23-.126-.003-. | 1 | | | | | | |
| *Oligota pusillima* | Staphylinidae | 23-.126-.008-. | 2 | | | | | | |
| *Opilo mollis* | Cleridae | 31-.006-.002-. | 1 | | | | | | |
| *Orchesia micans* | Melandryidae | 80-.005-.002-. | 2 | | | | | NT | |
| *Orthocis vestitus* | Ciidae | 65-.0061.007-. | 1 | | | | | | |
| *Orthoperus atomus* | Corylophidae | 601.008-.003-. | | 1 | 2 | | | | |
| *Orthoperus mundus* | Corylophidae | 601.008-.004-. | 2 | | 2 | | | | |
| *Orthoperus nigrescens* | Corylophidae | 601.008-.008-. | 5 | | 38 | 2 | | DD | |
| *Othius punctulatus* | Staphylinidae | 23-.082-.001-. | 2 | | | | | | |
| *Otiorhynchus singularis* | Curculionidae | 93-.015-.104-. | | 2 | | | | | |
| *Otiorhynchus subdentatus* | Curculionidae | 93-.015-.108-. | | 1 | | | | | |
| *Oxypoda alternans* | Staphylinidae | 23-.223-.034-. | 1 | | 1 | | | | |
| *Paromalus flavicornis* | Histeridae | 10-.020-.001-. | | | 1 | | | | |
| *Paromalus flavipes* | Histeridae | | 1 | | | | | | |
| *Pediacus depressus* | Cucujidae | 53-.015-.001-. | | | 2 | | | | |
| *Philonthus decorus* | Staphylinidae | 23-.088-.029-. | 1 | | | | | | |
| *Philonthus subuliformis* | Staphylinidae | 23-.088-.006-. | | 1 | | | | | |
| *Philonthus succicola* | Staphylinidae | 23-.088-.026-. | 8 | | | | | | |
| *Phloeocharis subtilissima* | Staphylinidae | 23-.005-.001-. | | 2 | | | | | |
| *Phloeonomus minimus* | Staphylinidae | 23-.016-.007-. | 1 | | 1 | 2 | 3 | | |
| *Phloeophagus lignarius* | Curculionidae | 93-.079-.001-. | 2 | | 1 | | | NT | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Phloeopora teres* | Staphylinidae | 23-.201-.001-. | 1 | | | 3 | 3 | | |
| *Phloeostiba lapponica* | Staphylinidae | 23-.0162.002-. | 6 | | 1 | | | | |
| *Phloeostiba plana* | Staphylinidae | 23-.0162.001-. | 1 | | 4 | | | | |
| *Phosphuga atrata* | Silphidae | 12-.009-.001-. | 3 | | | | | | |
| *Phyllobius argentatus* | Curculionidae | 93-.021-.019-. | 2 | | | | | | |
| *Pityophagus ferrugineus* | Nitidulidae | 50-.022-.001-. | 4 | 3 | 1 | | | | |
| *Placonotus testaceus* | Laemophloeidae | 561.002-.001-. | 3 | | | | | | |
| *Placusa atrata* | Staphylinidae | 23-.132-.005-. | 2 | 1 | 2 | | | | |
| *Placusa depressa* | Staphylinidae | 23-.132-.002-. | 1 | | | | | | |
| *Placusa incompleta* | Staphylinidae | 23-.132-.004-. | 4 | | | 3 | 3 | DD | |
| *Placusa pumilio* | Staphylinidae | 23-.132-.006-. | 45 | 1 | 8 | | | | |
| *Placusa tachyporoides* | Staphylinidae | 23-.132-.003-. | 87 | 6 | 17 | | | | |
| *Platycis cosnardi* | Lycidae | 25-.004-.002-. | 1 | | | 2 | | 3 | |
| *Platyrhinus resinosus* | Anthribidae | 90-.001-.001-. | 1 | | | | | | |
| *Plegaderus dissectus* | Histeridae | 10-.002-.004-. | 3 | | | 3 | 3 | | |
| *Prionocyphon serricornis* | Scirtidae | 40-.004-.001-. | 85 | 73 | 7 | 3 | | UE | |
| *Prionus coriarius* | Cerambycidae | 87-.004-.001-. | 1 | | | | | | |
| *Prionychus melanarius* | Tenebrionidae | 82-.003-.002-. | | | 1 | 1 | | 2 | yes |
| *Procraerus tibialis* | Elateridae | 34-.004-.001-. | 1 | | | 2 | | 3 | yes |
| *Proteinus atomarius* | Staphylinidae | 23-.009-.005-. | 2 | | | | | | |
| *Ptenidium formicetorum* | Ptiliidae | 21-.002-.008-. | 1 | | 1 | | | | |
| *Ptenidium gressneri* | Ptiliidae | 21-.002-.001-. | 8 | 3 | 3 | 3 | 3 | 3 | yes |
| *Ptenidium intermedium* | Ptiliidae | 21-.002-.004-. | 1 | | | | | | |
| *Ptenidium pusillum* | Ptiliidae | 21-.002-.010-. | 1 | | | | | | |
| *Ptenidium turgidum* | Ptiliidae | 21-.002-.003-. | 1 | | | 3 | 3 | UE | yes |
| *Pteryx suturalis* | Ptiliidae | 21-.013-.001-. | 5 | 6 | 1 | | | | |
| *Ptilinus pectinicornis* | Anobiidae | 68-.014-.001-. | 8 | 13 | 6 | | | | |
| *Ptinella aptera* | Ptiliidae | 21-.012-.004-. | 4 | | 1 | | | | |
| *Ptinella limbata* | Ptiliidae | 21-.012-.002-. | 1 | | | | | | |
| *Ptinus subpilosus* | Ptinidae | 69-.008-.013-. | 1 | | | | | | |
| *Quedius brevicornis* | Staphylinidae | 23-.104-.014-. | 2 | | 1 | 3 | 3 | | yes |
| *Quedius cruentus* | Staphylinidae | 23-.104-.013-. | 8 | 2 | 2 | | | | |
| *Quedius invreae* | Staphylinidae | 23-.104-.011-. | | | 1 | 3 | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Quedius mesomelinus* | Staphylinidae | 23-.104-.016-. | 1 | 33 | 4 | | | | |
| *Quedius microps* | Staphylinidae | 23-.104-.004-. | 1 | | | 3 | | 3 | yes |
| *Quedius truncicola* | Staphylinidae | 23-.104-.002-. | 8 | | 2 | 3 | | NT | yes |
| *Quedius xanthopus* | Staphylinidae | 23-.104-.019-. | 1 | | 2 | | | | |
| *Rhagonycha atra* | Cantharidae | 27-.005-.010-. | | 1 | | | | | |
| *Rhagonycha lignosa* | Cantharidae | 27-.005-.008-. | 2 | | | | | | |
| *Rhagonycha translucida* | Cantharidae | 27-.005-.003-. | 1 | | | | | | |
| *Rhamnusium bicolor* | Cerambycidae | 87-.012-.001-. | 3 | | 4 | 2 | 2 | 2 | yes |
| *Rhinomias forticornis* | Curculionidae | 93-.025-.001-. | 3 | | 3 | | | | |
| *Rhizophagus bipustulatus* | Monotomidae | 52-.001-.009-. | 22 | 2 | 9 | | | | |
| *Rhizophagus depressus* | Monotomidae | 52-.001-.003-. | 1 | 1 | | | | | |
| *Rhizophagus dispar* | Monotomidae | 52-.001-.008-. | 3 | 9 | 1 | | | | |
| *Rhizophagus ferrugineus* | Monotomidae | 52-.001-.004-. | 4 | | | | | | |
| *Rhizophagus parvulus* | Monotomidae | 52-.001-.012-. | 1 | | | | 3 | | |
| *Rhizophagus perforatus* | Monotomidae | 52-.001-.006-. | 2 | | | | 3 | | |
| *Rhynchaenus fagi* | Curculionidae | 93-.180-.013-. | 1 | | | | | | |
| *Rhyncolus ater* | Curculionidae | 93-.078-.004-. | | 20 | | | | | |
| *Rugilus rufipes* | Staphylinidae | 23-.061-.003-. | 1 | | | | | | |
| *Salpingus planirostris* | Salpingidae | 711.006-.002-. | 1 | | | | | | |
| *Scaphisoma agaricinum* | Staphylinidae | 22-.003-.001-. | 1 | | 3 | | | | |
| *Sciodrepoides watsoni* | Leiodidae | 14-.010-.001-. | 8 | | | | | | |
| *Scraptia fuscula* | Scraptiidae | 73-.001-.003-. | 31 | | 2 | 3 | 3 | | |
| *Sericoderus lateralis* | Corylophidae | 601.004-.001-. | 5 | | 7 | | | | |
| *Silvanus bidentatus* | Silvanidae | 531.006-.001-. | 1 | | | | | | |
| *Simo hirticornis* | Curculionidae | 93-.018-.001-. | | 1 | | | | | |
| *Sitophilus oryzae* | Curculionidae | 93-.131-.002-. | 1 | | | | | | |
| *Soronia grisea* | Nitidulidae | 50-.013-.002-. | 1 | | | | | | |
| *Stenichnus collaris* | Scydmaenidae | 18-.007-.008-. | 2 | | | | | | |
| *Stenichnus godarti* | Scydmaenidae | 18-.007-.005-. | 1 | | | | | | |
| *Stenichnus scutellaris* | Scydmaenidae | 18-.007-.003-. | 1 | | | | | | |
| *Stenomax aeneus* | Tenebrionidae | 83-.039-.001-. | | | 15 | | | NT | |
| *Stephostethus angusticollis* | Latridiidae | 58-.0061.002-. | | 1 | | | | | |
| *Stereocorynes truncorum* | Curculionidae | 93-.081-.001-. | 8 | | 2 | | | | |

| Species | Family | Lucht/EDV Code | Ebrach [individuals] | Fichtelberg [individuals] | Kelheim [individuals] | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|---|---|
| *Stethorus punctillum* | Coccinellidae | 62-.009-.001-. | 1 | | | | | | |
| *Strophosoma melanogrammum* | Curculionidae | 93-.040-.002-. | 1 | | | | | | |
| *Sulcacis affinis* | Ciidae | 65-.005-.001-. | 1 | | | | | | |
| *Sulcacis fronticornis* | Ciidae | 65-.005-.003-. | 1 | | | | | | |
| *Symbiotes gibberosus* | Anamorphidae | 61-.003-.002-. | | | 1 | 2 | | | |
| *Taphrorychus bicolor* | Scolytidae | 91-.031-.003-. | 1 | | | | | | |
| *Thamiaraea cinnamomea* | Staphylinidae | 23-.194-.001-. | | | 2 | 3 | | | |
| *Thamiaraea hospita* | Staphylinidae | 23-.194-.002-. | 1 | | | 2 | 3 | | |
| *Thanasimus formicarius* | Cleridae | 31-.007-.001-. | 5 | | 2 | | | | |
| *Tillus elongatus* | Cleridae | 31-.002-.001-. | 5 | | | 3 | | | |
| *Tomoxia bucephala* | Mordellidae | 79-.001-.001-. | | | 5 | | | | |
| *Trimium brevicorne* | Staphylinidae | 24-.011-.001-. | 1 | | | | | | |
| *Trinodes hirtus* | Dermestidae | 45-.010-.001-. | | | 1 | 3 | | | |
| *Triplax russica* | Erotylidae | 54-.002-.003-. | 2 | | | | 3 | | |
| *Trixagus dermestoides* | Throscidae | 37-.001-.002-. | 1 | | 1 | | | | |
| *Xyleborus dispar* | Scolytidae | 91-.036-.001-. | 23 | 2 | 45 | | | | |
| *Xyleborus dryographus* | Scolytidae | 91-.036-.007-. | 9 | | | | | | |
| *Xyleborus germanus* | Scolytidae | 91-.036-.008-. | 1510 | 3 | 334 | | | | |
| *Xyleborus monographus* | Scolytidae | 91-.036-.005-. | 3 | | | | | | |
| *Xyleborus peregrinus* | Scolytidae | 91-.036-.010-. | 491 | | 13 | | | | |
| *Xyleborus saxeseni* | Scolytidae | 91-.036-.004-. | 888 | 1 | 111 | | | | |
| *Xyloterus domesticus* | Scolytidae | 91-.038-.001-. | 1 | 2 | 3 | | | | |
| *Xyloterus lineatus* | Scolytidae | 91-.038-.003-. | 1 | | | | | | |
| *Xyloterus signatus* | Scolytidae | 91-.038-.002-. | | | 2 | | | | |
| *Zyras lugens* | Staphylinidae | 23-.196-.010-. | 1 | | | | | | |
| **Total:** | | | 4157 | 435 | 1288 | | | | |

**Table A5. List of the examined tree hollows and the saproxylic beetle species found within.** Red List status of saproxylic beetle species according to the Red List of Germany (2021), the Red List of Bavaria (2005) and the Red List of Germany (1998). Ecological status as tree hollow specialist species according to Heinz Bussler (personal communication). 0 = extinct or lost, 1 = threatened with extinction, 2 = highly threatened, 3 = threatened, UE = threat of unknown extent, NT = near threatened, DD = data deficient.

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| B08 | Ebrach | 2018 | *Allecula morio* | 3 | 3 | 3 | yes |
| B08 | Ebrach | 2018 | *Allecula rhenana* | 2 |  | 2 | yes |
| B08 | Ebrach | 2018 | *Anaspis marginicollis* |  | 2 | DD |  |
| B08 | Ebrach | 2018 | *Anaspis ruficollis* | 2 | 2 |  |  |
| B08 | Ebrach | 2018 | *Cerophytum elateroides* | 2 | 2 | 2 |  |
| B08 | Ebrach | 2018 | *Crepidophorus mutilatus* | 2 | 1 | 2 | yes |
| B08 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| B08 | Ebrach | 2018 | *Gnathoncus buyssoni* |  |  |  |  |
| B08 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 |  |  |
| B08 | Ebrach | 2018 | *Hypebaeus flavipes* | 3 | 3 | 3 |  |
| B08 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 |  |
| B08 | Ebrach | 2018 | *Melanotus rufipes* |  |  |  |  |
| B08 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| B08 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| B11 | Ebrach | 2018 | *Aleochara sparsa* |  |  |  |  |
| B11 | Ebrach | 2018 | *Aleochara stichai* |  |  |  |  |
| B11 | Ebrach | 2018 | *Atheta nigricornis* |  |  |  |  |
| B11 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| B11 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| B11 | Ebrach | 2018 | *Litargus connexus* |  |  |  |  |
| B11 | Ebrach | 2018 | *Mycetophagus populi* | 2 | 2 | 3 |  |
| B11 | Ebrach | 2018 | *Placusa atrata* |  |  |  |  |
| B11 | Ebrach | 2018 | *Placusa pumilio* |  |  |  |  |
| B11 | Ebrach | 2018 | *Placusa tachyporoides* |  |  |  |  |
| B11 | Ebrach | 2018 | *Quedius cruentus* |  |  |  |  |
| B11 | Ebrach | 2018 | *Quedius truncicola* | 3 |  | NT | yes |
| B11 | Ebrach | 2018 | *Sericoderus lateralis* |  |  |  |  |
| B11 | Ebrach | 2018 | *Silvanus bidentatus* |  |  |  |  |
| B11 | Ebrach | 2018 | *Xyleborus dispar* |  |  |  |  |
| B11 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| B11 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| B11 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| B14 | Ebrach | 2018 | *Atheta nigricornis* |  |  |  |  |
| B14 | Ebrach | 2018 | *Cerophytum elateroides* | 2 | 2 | 2 |  |
| B14 | Ebrach | 2018 | *Mycetochara axillaris* | 2 | 2 | 2 | yes |
| B14 | Ebrach | 2018 | *Oligota granaria* |  |  |  |  |
| B14 | Ebrach | 2018 | *Placusa pumilio* |  |  |  |  |
| B14 | Ebrach | 2018 | *Placusa tachyporoides* |  |  |  |  |
| B14 | Ebrach | 2018 | *Ptilinus pectinicornis* |  |  |  |  |
| B14 | Ebrach | 2018 | *Rhizophagus dispar* |  |  |  |  |
| B14 | Ebrach | 2018 | *Stereocorynes truncorum* |  |  |  |  |
| B14 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| B14 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| B14 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| B17 | Ebrach | 2018 | *Aleochara sparsa* |  |  |  |  |
| B17 | Ebrach | 2018 | *Aleochara stichai* |  |  |  |  |
| B17 | Ebrach | 2018 | *Litargus connexus* |  |  |  |  |
| B17 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 |  | UE |  |
| B17 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| B17 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| B17 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| B20 | Ebrach | 2018 | *Anaspis rufilabris* | | | | |
| B20 | Ebrach | 2018 | *Bibloporus minutus* | | | | |
| B20 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| B20 | Ebrach | 2018 | *Ptilinus pectinicornis* | | | | |
| B20 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B20 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| B20 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B22 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| B22 | Ebrach | 2018 | *Dorcatoma dresdensis* | 3 | 3 | | |
| B22 | Ebrach | 2018 | *Dorcatoma substriata* | 2 | 2 | NT | |
| B22 | Ebrach | 2018 | *Malthodes pumilus* | | | | |
| B22 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| B22 | Ebrach | 2018 | *Plegaderus dissectus* | 3 | 3 | | |
| B22 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| B22 | Ebrach | 2018 | *Ptenidium turgidum* | 3 | 3 | UE | yes |
| B22 | Ebrach | 2018 | *Quedius truncicola* | 3 | | NT | yes |
| B22 | Ebrach | 2018 | *Scraptia fuscula* | 3 | 3 | | |
| B22 | Ebrach | 2018 | *Stereocorynes truncorum* | | | | |
| B22 | Ebrach | 2018 | *Triplax russica* | | 3 | | |
| B22 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B22 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| B23 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| B23 | Ebrach | 2018 | *Acalles roboris* | | | | |
| B23 | Ebrach | 2018 | *Acrotrichis brevipennis* | | | | |
| B23 | Ebrach | 2018 | *Acrotrichis montandonii* | | | | |
| B23 | Ebrach | 2018 | *Catops picipes* | | | | |
| B23 | Ebrach | 2018 | *Cryptophagus pilosus* | | | | |
| B23 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| B23 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | | 2 | yes |
| B23 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| B23 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| B23 | Ebrach | 2018 | *Nicrophorus vespilloides* | | | | |
| B23 | Ebrach | 2018 | *Proteinus atomarius* | | | | |
| B23 | Ebrach | 2018 | *Thanasimus formicarius* | | | | |
| B23 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B23 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| B23 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B27 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| B27 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| B27 | Ebrach | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| B27 | Ebrach | 2018 | *Crepidophorus mutilatus* | 2 | 1 | 2 | yes |
| B27 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| B27 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| B27 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| B27 | Ebrach | 2018 | *Margarinotus striola* | | | | |
| B27 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| B27 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| B27 | Ebrach | 2018 | *Quedius truncicola* | 3 | | NT | yes |
| B27 | Ebrach | 2018 | *Scraptia fuscula* | 3 | 3 | | |
| B27 | Ebrach | 2018 | *Stereocorynes truncorum* | | | | |
| B27 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B27 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B29 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| B29 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| B29 | Ebrach | 2018 | *Dasytes cyaneus* | | | | |
| B29 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| B29 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| B29 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| B29 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| B29 | Ebrach | 2018 | *Pteryx suturalis* | | | | |
| B29 | Ebrach | 2018 | *Sciodrepoides watsoni* | | | | |
| B29 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B29 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B31 | Ebrach | 2018 | *Orthoperus mundus* | | | | |
| B31 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| B31 | Ebrach | 2018 | *Rhynchaenus fagi* | | | | |
| B31 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B31 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| B31 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B37 | Ebrach | 2018 | *Allecula morio* | 3 | 3 | 3 | yes |
| B37 | Ebrach | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| B37 | Ebrach | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| B37 | Ebrach | 2018 | *Cryptophagus thomsoni* | | | | |
| B37 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| B37 | Ebrach | 2018 | *Euplectus karstenii* | | | | |
| B37 | Ebrach | 2018 | *Haploglossa villosula* | | | | |
| B37 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| B37 | Ebrach | 2018 | *Hypebaeus flavipes* | 3 | 3 | 3 | |
| B37 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| B37 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| B37 | Ebrach | 2018 | *Orthoperus nigrescens* | 2 | | DD | |
| B37 | Ebrach | 2018 | *Phyllobius argentatus* | | | | |
| B37 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| B37 | Ebrach | 2018 | *Ptilinus pectinicornis* | | | | |
| B37 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B37 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B37 | Ebrach | 2018 | *Zyras lugens* | | | | |
| B38 | Ebrach | 2018 | *Phloeostiba plana* | | | | |
| B38 | Ebrach | 2018 | *Placusa incompleta* | 3 | 3 | DD | |
| B38 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B38 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| B38 | Ebrach | 2018 | *Xyloterus domesticus* | | | | |
| B40 | Ebrach | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| B40 | Ebrach | 2018 | *Cerophytum elateroides* | 2 | 2 | 2 | |
| B40 | Ebrach | 2018 | *Enicmus rugosus* | | | | |
| B40 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| B40 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| B40 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| B40 | Ebrach | 2018 | *Neuraphes praeteritus* | | | | |
| B40 | Ebrach | 2018 | *Pityophagus ferrugineus* | | | | |
| B40 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| B40 | Ebrach | 2018 | *Plegaderus dissectus* | 3 | 3 | | |
| B40 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| B40 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| B40 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S01 | Ebrach | 2018 | *Ampedus pomorum* | | | | |
| S01 | Ebrach | 2018 | *Anaglyptus mysticus* | | | | |
| S01 | Ebrach | 2018 | *Anaspis flava* | | | | |
| S01 | Ebrach | 2018 | *Anaspis thoracica* | | | | |
| S01 | Ebrach | 2018 | *Bryaxis puncticollis* | | | | |
| S01 | Ebrach | 2018 | *Cerophytum elateroides* | 2 | 2 | 2 | |
| S01 | Ebrach | 2018 | *Corymbia scutellata* | | 2 | 3 | |
| S01 | Ebrach | 2018 | *Dorcus parallelipipedus* | | | | |
| S01 | Ebrach | 2018 | *Echinodera hypocrita* | | | | |
| S01 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S01 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| S01 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S01 | Ebrach | 2018 | *Ischnomera caerulea* | 3 | | UE | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S01 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| S01 | Ebrach | 2018 | *Lagria atripes* | | | | |
| S01 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| S01 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S01 | Ebrach | 2018 | *Nalassus laevioctostriatus* | | | | |
| S01 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S01 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S01 | Ebrach | 2018 | *Ptilinus pectinicornis* | | | | |
| S01 | Ebrach | 2018 | *Scraptia fuscula* | 3 | 3 | | |
| S01 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S01 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S01 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S02 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S02 | Ebrach | 2018 | *Anobium nitidum* | | | | |
| S02 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S02 | Ebrach | 2018 | *Quedius cruentus* | | | | |
| S02 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S02 | Ebrach | 2018 | *Soronia grisea* | | | | |
| S02 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S02 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S02 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S03 | Ebrach | 2018 | *Acrotrichis montandonii* | | | | |
| S03 | Ebrach | 2018 | *Allecula rhenana* | 2 | | 2 | yes |
| S03 | Ebrach | 2018 | *Anaglyptus mysticus* | | | | |
| S03 | Ebrach | 2018 | *Anthobium atrocephalum* | | | | |
| S03 | Ebrach | 2018 | *Cryptophagus deubeli* | 1 | 1 | | |
| S03 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S03 | Ebrach | 2018 | *Dorcus parallelipipedus* | | | | |
| S03 | Ebrach | 2018 | *Echinodera hypocrita* | | | | |
| S03 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| S03 | Ebrach | 2018 | *Homoeusa acuminata* | | | | |
| S03 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S03 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S03 | Ebrach | 2018 | *Phosphuga atrata* | | | | |
| S03 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S03 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S03 | Ebrach | 2018 | *Rhinomias forticornis* | | | | |
| S03 | Ebrach | 2018 | *Thanasimus formicarius* | | | | |
| S03 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S03 | Ebrach | 2018 | *Xyleborus monographus* | | | | |
| S03 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S03 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S04 | Ebrach | 2018 | *Anthribus albinus* | | | | |
| S04 | Ebrach | 2018 | *Cryptophagus pallidus* | | | | |
| S04 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S04 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S05 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S05 | Ebrach | 2018 | *Anaglyptus mysticus* | | | | |
| S05 | Ebrach | 2018 | *Anaspis thoracica* | | | | |
| S05 | Ebrach | 2018 | *Bolitochara obliqua* | | | | |
| S05 | Ebrach | 2018 | *Clytus arietis* | | | | |
| S05 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S05 | Ebrach | 2018 | *Mycetophagus piceus* | 3 | 3 | NT | |
| S05 | Ebrach | 2018 | *Scraptia fuscula* | 3 | 3 | | |
| S05 | Ebrach | 2018 | *Triplax russica* | | 3 | | |
| S05 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S05 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S05 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S06 | Ebrach | 2018 | *Aleochara sparsa* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S06 | Ebrach | 2018 | *Anthribus albinus* | | | | |
| S06 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S06 | Ebrach | 2018 | *Leptusa fumida* | | | | |
| S06 | Ebrach | 2018 | *Mycetochara linearis* | | | | |
| S06 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S06 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S06 | Ebrach | 2018 | *Rhinomias forticornis* | | | | |
| S06 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S06 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S06 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S06 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S07 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S07 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S07 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S07 | Ebrach | 2018 | *Quedius brevicornis* | 3 | 3 | | yes |
| S07 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S07 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S09 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S09 | Ebrach | 2018 | *Cryptophagus pilosus* | | | | |
| S09 | Ebrach | 2018 | *Haploglossa villosula* | | | | |
| S09 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S09 | Ebrach | 2018 | *Melanotus castanipes* | | | | |
| S09 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S09 | Ebrach | 2018 | *Othius punctulatus* | | | | |
| S09 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S09 | Ebrach | 2018 | *Quedius brevicornis* | 3 | 3 | | yes |
| S09 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S09 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S09 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S10 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S10 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S10 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S10 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S10 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S10 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| S10 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| S10 | Ebrach | 2018 | *Placonotus testaceus* | | | | |
| S10 | Ebrach | 2018 | *Rhamnusium bicolor* | 2 | 2 | 2 | yes |
| S10 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S10 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S10 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S11 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S11 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S11 | Ebrach | 2018 | *Atheta britanniae* | | | | |
| S11 | Ebrach | 2018 | *Athous subfuscus* | | | | |
| S11 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S11 | Ebrach | 2018 | *Dalopius marginatus* | | | | |
| S11 | Ebrach | 2018 | *Hedobia imperialis* | | | | |
| S11 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S11 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| S11 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S11 | Ebrach | 2018 | *Orthoperus nigrescens* | 2 | | DD | |
| S11 | Ebrach | 2018 | *Phloeopora teres* | 3 | 3 | | |
| S11 | Ebrach | 2018 | *Pityophagus ferrugineus* | | | | |
| S11 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S11 | Ebrach | 2018 | *Rhizophagus dispar* | | | | |
| S11 | Ebrach | 2018 | *Sericoderus lateralis* | | | | |
| S11 | Ebrach | 2018 | *Taphrorychus bicolor* | | | | |
| S11 | Ebrach | 2018 | *Xyleborus dispar* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S11 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S11 | Ebrach | 2018 | *Xyleborus monographus* | | | | |
| S11 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S12 | Ebrach | 2018 | *Ampedus pomorum* | | | | |
| S12 | Ebrach | 2018 | *Anisotoma castanea* | | | | |
| S12 | Ebrach | 2018 | *Anisotoma humeralis* | | | | |
| S12 | Ebrach | 2018 | *Anisotoma orbicularis* | | | | |
| S12 | Ebrach | 2018 | *Arpidiphorus orbiculatus* | | | | |
| S12 | Ebrach | 2018 | *Echinodera hypocrita* | | | | |
| S12 | Ebrach | 2018 | *Enicmus rugosus* | | | | |
| S12 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S12 | Ebrach | 2018 | *Leptusa fumida* | | | | |
| S12 | Ebrach | 2018 | *Malachius bipustulatus* | | | | |
| S12 | Ebrach | 2018 | *Mycetophagus populi* | 2 | 2 | 3 | |
| S12 | Ebrach | 2018 | *Platyrhinus resinosus* | | | | |
| S12 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| S12 | Ebrach | 2018 | *Ptinus subpilosus* | | | | |
| S12 | Ebrach | 2018 | *Rhizophagus perforatus* | | 3 | | |
| S12 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S12 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S12 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S13 | Ebrach | 2018 | *Atheta pallidicornis* | | | | |
| S13 | Ebrach | 2018 | *Atheta picipes* | | | | |
| S13 | Ebrach | 2018 | *Batrisus formicarius* | | | NT | |
| S13 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S13 | Ebrach | 2018 | *Malthodes sp.* | | | | |
| S13 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S13 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S13 | Ebrach | 2018 | *Stenichnus godarti* | | | | |
| S13 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S14 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S14 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S14 | Ebrach | 2018 | *Atheta nigricornis* | | | | |
| S14 | Ebrach | 2018 | *Athous subfuscus* | | | | |
| S14 | Ebrach | 2018 | *Cis nitidus* | | | | |
| S14 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S14 | Ebrach | 2018 | *Glischrochilus hortensis* | | | | |
| S14 | Ebrach | 2018 | *Habrocerus capillaricornis* | | | | |
| S14 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S14 | Ebrach | 2018 | *Oxypoda alternans* | | | | |
| S14 | Ebrach | 2018 | *Philonthus succicola* | | | | |
| S14 | Ebrach | 2018 | *Placonotus testaceus* | | | | |
| S14 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S14 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S14 | Ebrach | 2018 | *Quedius cruentus* | | | | |
| S14 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S14 | Ebrach | 2018 | *Thamiaraea hospita* | 2 | 3 | | |
| S14 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S14 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S14 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S14 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S15 | Ebrach | 2018 | *Ampedus erythrogonus* | 3 | 3 | 3 | |
| S15 | Ebrach | 2018 | *Phloeophagus lignarius* | | | NT | |
| S15 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S15 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S15 | Ebrach | 2018 | *Stereocorynes truncorum* | | | | |
| S15 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S16 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S16 | Ebrach | 2018 | *Barypeithes pellucidus* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S16 | Ebrach | 2018 | *Ischnomera caerulea* | 3 |  | UE |  |
| S16 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| S16 | Ebrach | 2018 | *Litargus connexus* |  |  |  |  |
| S16 | Ebrach | 2018 | *Placusa pumilio* |  |  |  |  |
| S16 | Ebrach | 2018 | *Placusa tachyporoides* |  |  |  |  |
| S16 | Ebrach | 2018 | *Quedius truncicola* | 3 |  | NT |  |
| S16 | Ebrach | 2018 | *Rhinomias forticornis* |  |  |  |  |
| S16 | Ebrach | 2018 | *Strophosoma melanogrammum* |  |  |  |  |
| S16 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| S16 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| S16 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| S17 | Ebrach | 2018 | *Aleochara sparsa* |  |  |  |  |
| S17 | Ebrach | 2018 | *Aleochara stichai* |  |  |  |  |
| S17 | Ebrach | 2018 | *Cryptophagus dentatus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Euplectus karstenii* |  |  |  |  |
| S17 | Ebrach | 2018 | *Malthodes marginatus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Placusa depressa* |  |  |  |  |
| S17 | Ebrach | 2018 | *Placusa incompleta* | 3 | 3 | DD |  |
| S17 | Ebrach | 2018 | *Placusa pumilio* |  |  |  |  |
| S17 | Ebrach | 2018 | *Placusa tachyporoides* |  |  |  |  |
| S17 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 |  | UE |  |
| S17 | Ebrach | 2018 | *Rhizophagus bipustulatus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Rhizophagus depressus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Salpingus planirostris* |  |  |  |  |
| S17 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Xyleborus peregrinus* |  |  |  |  |
| S17 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| S19 | Ebrach | 2018 | *Abraeus perpusillus* |  |  |  |  |
| S19 | Ebrach | 2018 | *Aleochara sparsa* |  |  |  |  |
| S19 | Ebrach | 2018 | *Ampedus pomorum* |  |  |  |  |
| S19 | Ebrach | 2018 | *Atheta sodalis* |  |  |  |  |
| S19 | Ebrach | 2018 | *Cantharis decipiens* |  |  |  |  |
| S19 | Ebrach | 2018 | *Cryptophagus pilosus* |  |  |  |  |
| S19 | Ebrach | 2018 | *Cryptophagus scanicus* |  |  |  |  |
| S19 | Ebrach | 2018 | *Dienerella clathrata* |  |  |  |  |
| S19 | Ebrach | 2018 | *Melanotus rufipes* |  |  |  |  |
| S19 | Ebrach | 2018 | *Orthoperus nigrescens* | 2 |  | DD |  |
| S19 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 |  | UE |  |
| S19 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| S19 | Ebrach | 2018 | *Ptenidium pusillum* |  |  |  |  |
| S19 | Ebrach | 2018 | *Rhagonycha lignosa* |  |  |  |  |
| S19 | Ebrach | 2018 | *Sericoderus lateralis* |  |  |  |  |
| S19 | Ebrach | 2018 | *Xyleborus dispar* |  |  |  |  |
| S19 | Ebrach | 2018 | *Xyleborus germanus* |  |  |  |  |
| S19 | Ebrach | 2018 | *Xyleborus saxeseni* |  |  |  |  |
| S20 | Ebrach | 2018 | *Aleochara sparsa* |  |  |  |  |
| S20 | Ebrach | 2018 | *Atheta britanniae* |  |  |  |  |
| S20 | Ebrach | 2018 | *Atheta pallidicornis* |  |  |  |  |
| S20 | Ebrach | 2018 | *Cis fusciclavis* |  |  |  |  |
| S20 | Ebrach | 2018 | *Clambus punctulum* |  |  |  |  |
| S20 | Ebrach | 2018 | *Cryptophagus dentatus* |  |  |  |  |
| S20 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 |  |  |
| S20 | Ebrach | 2018 | *Melanotus castanipes* |  |  |  |  |
| S20 | Ebrach | 2018 | *Microscydmus minimus* | 3 |  |  |  |
| S20 | Ebrach | 2018 | *Placusa incompleta* | 3 | 3 | DD |  |
| S20 | Ebrach | 2018 | *Placusa tachyporoides* |  |  |  |  |
| S20 | Ebrach | 2018 | *Plegaderus dissectus* | 3 | 3 |  |  |
| S20 | Ebrach | 2018 | *Pteryx suturalis* |  |  |  |  |
| S20 | Ebrach | 2018 | *Xyleborus dispar* |  |  |  |  |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S20 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S20 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S20 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S21 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S21 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S21 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S21 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S21 | Ebrach | 2018 | *Ptenidium formicetorum* | | | | |
| S21 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S21 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S21 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S22 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S22 | Ebrach | 2018 | *Dalopius marginatus* | | | | |
| S22 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S22 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| S22 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S22 | Ebrach | 2018 | *Othius punctulatus* | | | | |
| S22 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| S22 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S22 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S22 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S23 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S23 | Ebrach | 2018 | *Anaglyptus mysticus* | | | | |
| S23 | Ebrach | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| S23 | Ebrach | 2018 | *Anobium nitidum* | | | | |
| S23 | Ebrach | 2018 | *Cryptolestes minutus* | | | | |
| S23 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S23 | Ebrach | 2018 | *Ischnomera caerulea* | 3 | | UE | |
| S23 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S23 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S23 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S23 | Ebrach | 2018 | *Quedius cruentus* | | | | |
| S23 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S23 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S23 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S24 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S24 | Ebrach | 2018 | *Ampedus brunnicornis* | 1 | 1 | 1 | |
| S24 | Ebrach | 2018 | *Haploglossa villosula* | | | | |
| S24 | Ebrach | 2018 | *Ischnomera sanguinicollis* | 3 | 2 | 3 | yes |
| S24 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S24 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S24 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S24 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S24 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S24 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S25 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| S25 | Ebrach | 2018 | *Ampedus pomorum* | | | | |
| S25 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S25 | Ebrach | 2018 | *Ennearthron cornutum* | | | | |
| S25 | Ebrach | 2018 | *Mycetophagus quadripustulatus* | | | | |
| S25 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S25 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S25 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S26 | Ebrach | 2018 | *Atheta nigricornis* | | | | |
| S26 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S26 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S26 | Ebrach | 2018 | *Gnathoncus buyssoni* | | | | |
| S26 | Ebrach | 2018 | *Mycetochara linearis* | | | | |
| S26 | Ebrach | 2018 | *Nalassus laevioctostriatus* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S26 | Ebrach | 2018 | *Orthocis vestitus* | | | | |
| S26 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S26 | Ebrach | 2018 | *Stenichnus collaris* | | | | |
| S26 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S26 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S26 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S27 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| S27 | Ebrach | 2018 | *Atheta nigricornis* | | | | |
| S27 | Ebrach | 2018 | *Nalassus laevioctostriatus* | | | | |
| S27 | Ebrach | 2018 | *Pityophagus ferrugineus* | | | | |
| S27 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S27 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S27 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S27 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S28 | Ebrach | 2018 | *Allecula rhenana* | 2 | | 2 | yes |
| S28 | Ebrach | 2018 | *Anaglyptus mysticus* | | | | |
| S28 | Ebrach | 2018 | *Atomaria nigrirostris* | | | | |
| S28 | Ebrach | 2018 | *Brachysomus echinatus* | | | | |
| S28 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S28 | Ebrach | 2018 | *Lordithon trinotatus* | | | | |
| S28 | Ebrach | 2018 | *Nalassus laevioctostriatus* | | | | |
| S28 | Ebrach | 2018 | *Neuraphes plicicollis* | | | | |
| S28 | Ebrach | 2018 | *Orthoperus mundus* | | | | |
| S28 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S28 | Ebrach | 2018 | *Rhizophagus perforatus* | | 3 | | |
| S28 | Ebrach | 2018 | *Stereocorynes truncorum* | | | | |
| S28 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S29 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S29 | Ebrach | 2018 | *Atheta nigricornis* | | | | |
| S29 | Ebrach | 2018 | *Nalassus laevioctostriatus* | | | | |
| S29 | Ebrach | 2018 | *Phloeostiba lapponica* | | | | |
| S29 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S29 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S29 | Ebrach | 2018 | *Quedius cruentus* | | | | |
| S29 | Ebrach | 2018 | *Quedius mesomelinus* | | | | |
| S29 | Ebrach | 2018 | *Quedius xanthopus* | | | | |
| S29 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S29 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S29 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S30 | Ebrach | 2018 | *Alosterna tabacicolor* | | | | |
| S30 | Ebrach | 2018 | *Atheta sodalis* | | | | |
| S30 | Ebrach | 2018 | *Leptusa ruficollis* | | | | |
| S30 | Ebrach | 2018 | *Melanotus castanipes* | | | | |
| S30 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S30 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S30 | Ebrach | 2018 | *Orthoperus nigrescens* | 2 | | DD | |
| S30 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S30 | Ebrach | 2018 | *Scaphisoma agaricinum* | | | | |
| S30 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S30 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S30 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S31 | Ebrach | 2018 | *Agathidium seminulum* | | | | |
| S31 | Ebrach | 2018 | *Allecula morio* | 3 | 3 | 3 | yes |
| S31 | Ebrach | 2018 | *Ampedus balteatus* | | | | |
| S31 | Ebrach | 2018 | *Ampedus pomorum* | | | | |
| S31 | Ebrach | 2018 | *Apocatops nigrita* | | | | |
| S31 | Ebrach | 2018 | *Arpidiphorus orbiculatus* | | | | |
| S31 | Ebrach | 2018 | *Catops neglectus* | | | | |
| S31 | Ebrach | 2018 | *Cerylon fagi* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S31 | Ebrach | 2018 | *Cis glabratus* | 3 | | | |
| S31 | Ebrach | 2018 | *Cryptophagus pilosus* | | | | |
| S31 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S31 | Ebrach | 2018 | *Dinaraea linearis* | | | | |
| S31 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S31 | Ebrach | 2018 | *Leptusa fumida* | | | | |
| S31 | Ebrach | 2018 | *Lordithon trinotatus* | | | | |
| S31 | Ebrach | 2018 | *Malthinus punctatus* | | | | |
| S31 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S31 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S31 | Ebrach | 2018 | *Nicrophorus vespilloides* | | | | |
| S31 | Ebrach | 2018 | *Philonthus succicola* | | | | |
| S31 | Ebrach | 2018 | *Phloeostiba lapponica* | | | | |
| S31 | Ebrach | 2018 | *Phosphuga atrata* | | | | |
| S31 | Ebrach | 2018 | *Proteinus atomarius* | | | | |
| S31 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S31 | Ebrach | 2018 | *Sericoderus lateralis* | | | | |
| S31 | Ebrach | 2018 | *Stethorus punctillum* | | | | |
| S31 | Ebrach | 2018 | *Trixagus dermestoides* | | | | |
| S31 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S31 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S31 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S32 | Ebrach | 2018 | *Aulonothroscus brevicollis* | | | | |
| S32 | Ebrach | 2018 | *Cryptolestes ferrugineus* | | | | |
| S32 | Ebrach | 2018 | *Cryptophagus pallidus* | | | | |
| S32 | Ebrach | 2018 | *Cryptophagus scanicus* | | | | |
| S32 | Ebrach | 2018 | *Dienerella clathrata* | | | | |
| S32 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| S32 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S32 | Ebrach | 2018 | *Melanotus castanipes* | | | | |
| S32 | Ebrach | 2018 | *Nemosoma elongatum* | | | | |
| S32 | Ebrach | 2018 | *Orchesia micans* | | | NT | |
| S32 | Ebrach | 2018 | *Phosphuga atrata* | | | | |
| S32 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S32 | Ebrach | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| S32 | Ebrach | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| S32 | Ebrach | 2018 | *Scraptia fuscula* | 3 | 3 | | |
| S32 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S32 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S32 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S33 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S33 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S33 | Ebrach | 2018 | *Atheta britanniae* | | | | |
| S33 | Ebrach | 2018 | *Atheta nigricornis* | | | | |
| S33 | Ebrach | 2018 | *Atheta pallidicornis* | | | | |
| S33 | Ebrach | 2018 | *Athous subfuscus* | | | | |
| S33 | Ebrach | 2018 | *Cephennium thoracicum* | | | | |
| S33 | Ebrach | 2018 | *Corticarina obfuscata* | 2 | 2 | DD | |
| S33 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S33 | Ebrach | 2018 | *Dasycerus sulcatus* | | | | |
| S33 | Ebrach | 2018 | *Echinodera hypocrita* | | | | |
| S33 | Ebrach | 2018 | *Euplectus karstenii* | | | | |
| S33 | Ebrach | 2018 | *Holobus apicatus* | 3 | 3 | | |
| S33 | Ebrach | 2018 | *Lordithon exoletus* | | | | |
| S33 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S33 | Ebrach | 2018 | *Mycetophagus atomarius* | | | | |
| S33 | Ebrach | 2018 | *Phloeonomus minimus* | 2 | 3 | | |
| S33 | Ebrach | 2018 | *Phloeostiba lapponica* | | | | |
| S33 | Ebrach | 2018 | *Pityophagus ferrugineus* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S33 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S33 | Ebrach | 2018 | *Prionus coriarius* | | | | |
| S33 | Ebrach | 2018 | *Pteryx suturalis* | | | | |
| S33 | Ebrach | 2018 | *Ptilinus pectinicornis* | | | | |
| S33 | Ebrach | 2018 | *Quedius truncicola* | 3 | | NT | yes |
| S33 | Ebrach | 2018 | *Sitophilus oryzae* | | | | |
| S33 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S33 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S33 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S33 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S36 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| S36 | Ebrach | 2018 | *Cerylon fagi* | | | | |
| S36 | Ebrach | 2018 | *Cerylon histeroides* | | | | |
| S36 | Ebrach | 2018 | *Cryptophagus dentatus* | | | | |
| S36 | Ebrach | 2018 | *Euplectus nanus* | | | | |
| S36 | Ebrach | 2018 | *Phloeostiba lapponica* | | | | |
| S36 | Ebrach | 2018 | *Placonotus testaceus* | | | | |
| S36 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S36 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S36 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S45 | Ebrach | 2018 | *Hesperus rufipennis* | 2 | 0 | 2 | yes |
| S45 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S46 | Ebrach | 2018 | *Abraeus perpusillus* | | | | |
| S46 | Ebrach | 2018 | *Allecula rhenana* | 2 | | 2 | yes |
| S46 | Ebrach | 2018 | *Anaspis thoracica* | | | | |
| S46 | Ebrach | 2018 | *Arpidiphorus orbiculatus* | | | | |
| S46 | Ebrach | 2018 | *Cerophytum elateroides* | 2 | 2 | 2 | |
| S46 | Ebrach | 2018 | *Cis boleti* | | | | |
| S46 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| S46 | Ebrach | 2018 | *Euplectus karstenii* | | | | |
| S46 | Ebrach | 2018 | *Euplectus punctatus* | | | | |
| S46 | Ebrach | 2018 | *Hapalaraea pygmaea* | 3 | 3 | | |
| S46 | Ebrach | 2018 | *Ischnomera caerulea* | 3 | | UE | |
| S46 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S46 | Ebrach | 2018 | *Mycetophagus populi* | 2 | 2 | 3 | |
| S46 | Ebrach | 2018 | *Paromalus flavipes* | | | | |
| S46 | Ebrach | 2018 | *Placusa incompleta* | 3 | 3 | DD | |
| S46 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S46 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S46 | Ebrach | 2018 | *Ptinella aptera* | | | | |
| S46 | Ebrach | 2018 | *Ptinella limbata* | | | | |
| S46 | Ebrach | 2018 | *Sulcacis affinis* | | | | |
| S46 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S46 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S46 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S47 | Ebrach | 2018 | *Aleochara sparsa* | | | | |
| S47 | Ebrach | 2018 | *Aleochara stichai* | | | | |
| S47 | Ebrach | 2018 | *Microscydmus minimus* | 3 | | | |
| S47 | Ebrach | 2018 | *Placusa atrata* | | | | |
| S47 | Ebrach | 2018 | *Placusa pumilio* | | | | |
| S47 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S47 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S47 | Ebrach | 2018 | *Rhizophagus parvulus* | | 3 | | |
| S47 | Ebrach | 2018 | *Thanasimus formicarius* | | | | |
| S47 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S47 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S47 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S48 | Ebrach | 2018 | *Athous subfuscus* | | | | |
| S48 | Ebrach | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| S48 | Ebrach | 2018 | *Melanotus rufipes* | | | | |
| S48 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S48 | Ebrach | 2018 | *Pteryx suturalis* | | | | |
| S48 | Ebrach | 2018 | *Quedius truncicola* | 3 | | NT | yes |
| S48 | Ebrach | 2018 | *Rhizophagus bipustulatus* | | | | |
| S48 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S48 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| S49 | Ebrach | 2018 | *Acrotrichis sp.* | | | | |
| S49 | Ebrach | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| S49 | Ebrach | 2018 | *Aulonothroscus brevicollis* | | | | |
| S49 | Ebrach | 2018 | *Corticaria alleni* | 2 | | DD | |
| S49 | Ebrach | 2018 | *Malthodes marginatus* | | | | |
| S49 | Ebrach | 2018 | *Placusa tachyporoides* | | | | |
| S49 | Ebrach | 2018 | *Sericoderus lateralis* | | | | |
| S49 | Ebrach | 2018 | *Xyleborus dispar* | | | | |
| S49 | Ebrach | 2018 | *Xyleborus germanus* | | | | |
| S49 | Ebrach | 2018 | *Xyleborus monographus* | | | | |
| S49 | Ebrach | 2018 | *Xyleborus peregrinus* | | | | |
| S49 | Ebrach | 2018 | *Xyleborus saxeseni* | | | | |
| F02 | Fichtelberg | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| F02 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F02 | Fichtelberg | 2018 | *Athous subfuscus* | | | | |
| F02 | Fichtelberg | 2018 | *Cryptophagus deubeli* | 1 | 1 | | |
| F02 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F02 | Fichtelberg | 2018 | *Epuraea variegata* | | | | |
| F02 | Fichtelberg | 2018 | *Malthodes sp.* | | | | |
| F02 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F02 | Fichtelberg | 2018 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| F02 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F06 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F06 | Fichtelberg | 2018 | *Brachytarsus nebulosus* | | | | |
| F06 | Fichtelberg | 2018 | *Otiorhynchus subdentatus* | | | | |
| F08 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F08 | Fichtelberg | 2018 | *Pteryx suturalis* | | | | |
| F09 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F09 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F09 | Fichtelberg | 2018 | *Hylastes cunicularius* | | | | |
| F09 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F09 | Fichtelberg | 2018 | *Otiorhynchus singularis* | | | | |
| F09 | Fichtelberg | 2018 | *Placusa tachyporoides* | | | | |
| F09 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F11 | Fichtelberg | 2018 | *Atheta fungi* | | | | |
| F11 | Fichtelberg | 2018 | *Epuraea pygmaea* | | | | |
| F11 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| F12 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F12 | Fichtelberg | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| F12 | Fichtelberg | 2018 | *Gnathoncus buyssoni* | | | | |
| F12 | Fichtelberg | 2018 | *Phloeocharis subtilissima* | | | | |
| F12 | Fichtelberg | 2018 | *Placusa tachyporoides* | | | | |
| F12 | Fichtelberg | 2018 | *Rhyncolus ater* | | | | |
| F13 | Fichtelberg | 2018 | *Hylastes cunicularius* | | | | |
| F13 | Fichtelberg | 2018 | *Malthinus punctatus* | | | | |
| F13 | Fichtelberg | 2018 | *Quedius cruentus* | | | | |
| F13 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F14 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F14 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F14 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F16 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F16 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| F16 | Fichtelberg | 2018 | *Cerylon ferrugineum* | | | | |
| F16 | Fichtelberg | 2018 | *Coryphium angusticolle* | | | | |
| F16 | Fichtelberg | 2018 | *Mniusa incrassata* | | | | |
| F16 | Fichtelberg | 2018 | *Placusa tachyporoides* | | | | |
| F16 | Fichtelberg | 2018 | *Pteryx suturalis* | | | | |
| F16 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| F16 | Fichtelberg | 2018 | *Xyleborus dispar* | | | | |
| F18 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F18 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F18 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F18 | Fichtelberg | 2018 | *Epuraea pygmaea* | | | | |
| F18 | Fichtelberg | 2018 | *Otiorhynchus singularis* | | | | |
| F18 | Fichtelberg | 2018 | *Pityophagus ferrugineus* | | | | |
| F18 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| F19 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F21 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F21 | Fichtelberg | 2018 | *Xyleborus saxeseni* | | | | |
| F22 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F22 | Fichtelberg | 2018 | *Anthophagus angusticollis* | | | | |
| F22 | Fichtelberg | 2018 | *Denticollis linearis* | | | | |
| F22 | Fichtelberg | 2018 | *Eusphalerum limbatum* | | | | |
| F22 | Fichtelberg | 2018 | *Eusphalerum signatum* | | | | |
| F22 | Fichtelberg | 2018 | *Malthodes guttifer* | | | | |
| F22 | Fichtelberg | 2018 | *Placusa tachyporoides* | | | | |
| F22 | Fichtelberg | 2018 | *Rhizophagus depressus* | | | | |
| F23 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F23 | Fichtelberg | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| F23 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F23 | Fichtelberg | 2018 | *Anthribus albinus* | | | | |
| F23 | Fichtelberg | 2018 | *Brachytarsus nebulosus* | | | | |
| F23 | Fichtelberg | 2018 | *Cortinicara gibbosa* | | | | |
| F23 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F23 | Fichtelberg | 2018 | *Leptura maculata* | | | | |
| F23 | Fichtelberg | 2018 | *Leptusa fumida* | | | | |
| F23 | Fichtelberg | 2018 | *Phloeocharis subtilissima* | | | | |
| F23 | Fichtelberg | 2018 | *Ptilinus pectinicornis* | | | | |
| F23 | Fichtelberg | 2018 | *Rhyncolus ater* | | | | |
| F23 | Fichtelberg | 2018 | *Xyleborus germanus* | | | | |
| F24 | Fichtelberg | 2018 | *Cartodere nodifer* | | | | |
| F25 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F25 | Fichtelberg | 2018 | *Malthodes marginatus* | | | | |
| F25 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F26 | Fichtelberg | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| F26 | Fichtelberg | 2018 | *Melanotus castanipes* | | | | |
| F27 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F27 | Fichtelberg | 2018 | *Bolitobius inclinans* | | | | |
| F27 | Fichtelberg | 2018 | *Hylastes cunicularius* | | | | |
| F27 | Fichtelberg | 2018 | *Hylecoetus dermestoides* | | | | |
| F27 | Fichtelberg | 2018 | *Lordithon exoletus* | | | | |
| F27 | Fichtelberg | 2018 | *Pityophagus ferrugineus* | | | | |
| F27 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F27 | Fichtelberg | 2018 | *Rhagonycha atra* | | | | |
| F28 | Fichtelberg | 2018 | *Clambus punctulum* | | | | |
| F28 | Fichtelberg | 2018 | *Lathrobium fulvipenne* | | | | |
| F28 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F29 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F29 | Fichtelberg | 2018 | *Haploglossa villosula* | | | | |
| F30 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F30 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| F30 | Fichtelberg | 2018 | *Philonthus subuliformis* | | | | |
| F31 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F31 | Fichtelberg | 2018 | *Atheta sodalis* | | | | |
| F31 | Fichtelberg | 2018 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| F33 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F33 | Fichtelberg | 2018 | *Cryptophagus labilis* | 2 | 2 | NT | yes |
| F33 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F33 | Fichtelberg | 2018 | *Hylastes cunicularius* | | | | |
| F33 | Fichtelberg | 2018 | *Ptilinus pectinicornis* | | | | |
| F33 | Fichtelberg | 2018 | *Rhizophagus bipustulatus* | | | | |
| F33 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| F34 | Fichtelberg | 2018 | *Anisotoma humeralis* | | | | |
| F34 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F34 | Fichtelberg | 2018 | *Placusa atrata* | | | | |
| F34 | Fichtelberg | 2018 | *Ptilinus pectinicornis* | | | | |
| F35 | Fichtelberg | 2018 | *Atheta coriaria* | | | | |
| F35 | Fichtelberg | 2018 | *Pteryx suturalis* | | | | |
| F36 | Fichtelberg | 2018 | *Melanotus castanipes* | | | | |
| F36 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F36 | Fichtelberg | 2018 | *Pteryx suturalis* | | | | |
| F36 | Fichtelberg | 2018 | *Rhyncolus ater* | | | | |
| F37 | Fichtelberg | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| F37 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F39 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F39 | Fichtelberg | 2018 | *Brachytarsus nebulosus* | | | | |
| F39 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F39 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F40 | Fichtelberg | 2018 | *Anaglyptus mysticus* | | | | |
| F40 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F40 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F40 | Fichtelberg | 2018 | *Haploglossa villosula* | | | | |
| F40 | Fichtelberg | 2018 | *Orthoperus atomus* | | | | |
| F40 | Fichtelberg | 2018 | *Rhyncolus ater* | | | | |
| F41 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F41 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F41 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F41 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F41 | Fichtelberg | 2018 | *Rhizophagus bipustulatus* | | | | |
| F42 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F42 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F42 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F44 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F44 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F44 | Fichtelberg | 2018 | *Catops tristis* | | | | |
| F44 | Fichtelberg | 2018 | *Clambus punctulum* | | | | |
| F44 | Fichtelberg | 2018 | *Cryptophagus deubeli* | 1 | 1 | | |
| F44 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F44 | Fichtelberg | 2018 | *Fissocatops westi* | | | | |
| F44 | Fichtelberg | 2018 | *Gnathoncus buyssoni* | | | | |
| F44 | Fichtelberg | 2018 | *Pityophagus ferrugineus* | | | | |
| F44 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F46 | Fichtelberg | 2018 | *Cis dentatus* | 3 | | | |
| F46 | Fichtelberg | 2018 | *Cryptophagus deubeli* | 1 | 1 | | |
| F46 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F46 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F46 | Fichtelberg | 2018 | *Placusa tachyporoides* | | | | |
| F46 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F46 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| F46 | Fichtelberg | 2018 | *Simo hirticornis* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| F47 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F47 | Fichtelberg | 2018 | *Leptusa fumida* | | | | |
| F47 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F47 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F48 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F48 | Fichtelberg | 2018 | *Ampedus erythrogonus* | 3 | 3 | 3 | |
| F48 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F48 | Fichtelberg | 2018 | *Malthodes sp.* | | | | |
| F48 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F48 | Fichtelberg | 2018 | *Stephostethus angusticollis* | | | | |
| F49 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F49 | Fichtelberg | 2018 | *Dryocoetes autographus* | | | | |
| F49 | Fichtelberg | 2018 | *Hylastes cunicularius* | | | | |
| F49 | Fichtelberg | 2018 | *Malthodes guttifer* | | | | |
| F50 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F50 | Fichtelberg | 2018 | *Placusa pumilio* | | | | |
| F50 | Fichtelberg | 2018 | *Xyleborus dispar* | | | | |
| F50 | Fichtelberg | 2018 | *Xyloterus domesticus* | | | | |
| F51 | Fichtelberg | 2018 | *Anaspis marginicollis* | | 2 | DD | |
| F51 | Fichtelberg | 2018 | *Anaspis ruficollis* | 2 | 2 | | |
| F51 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F51 | Fichtelberg | 2018 | *Brachytarsus nebulosus* | | | | |
| F52 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F52 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F52 | Fichtelberg | 2018 | *Quedius cruentus* | | | | |
| F53 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F53 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F53 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F54 | Fichtelberg | 2018 | *Atheta nigricornis* | | | | |
| F54 | Fichtelberg | 2018 | *Cryptophagus dentatus* | | | | |
| F54 | Fichtelberg | 2018 | *Dienerella elongata* | | | | |
| F54 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F54 | Fichtelberg | 2018 | *Pteryx suturalis* | | | | |
| F54 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F56 | Fichtelberg | 2018 | *Aleochara sparsa* | | | | |
| F56 | Fichtelberg | 2018 | *Melanotus rufipes* | | | | |
| F56 | Fichtelberg | 2018 | *Prionocyphon serricornis* | 3 | | UE | |
| F56 | Fichtelberg | 2018 | *Quedius mesomelinus* | | | | |
| F56 | Fichtelberg | 2018 | *Rhizophagus dispar* | | | | |
| K02 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K02 | Kelheim | 2019 | *Cryptophagus dentatus* | | | | |
| K02 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K02 | Kelheim | 2019 | *Scraptia fuscula* | 3 | 3 | | |
| K02 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K02 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K07 | Kelheim | 2019 | *Cryptophagus scanicus* | | | | |
| K07 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K07 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K07 | Kelheim | 2019 | *Ptenidium formicetorum* | | | | |
| K07 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K07 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K10 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K10 | Kelheim | 2019 | *Atheta nigricornis* | | | | |
| K10 | Kelheim | 2019 | *Cryptophagus scanicus* | | | | |
| K10 | Kelheim | 2019 | *Dienerella elongata* | | | | |
| K10 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K10 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K10 | Kelheim | 2019 | *Pediacus depressus* | | | | |
| K10 | Kelheim | 2019 | *Placusa pumilio* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K10 | Kelheim | 2019 | *Symbiotes gibberosus* | 2 | | | |
| K10 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K10 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K11 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K11 | Kelheim | 2019 | *Cryptophagus scanicus* | | | | |
| K11 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K11 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K11 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K11 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K12 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K12 | Kelheim | 2019 | *Ampedus balteatus* | | | | |
| K12 | Kelheim | 2019 | *Ampedus pomorum* | | | | |
| K12 | Kelheim | 2019 | *Anaspis thoracica* | | | | |
| K12 | Kelheim | 2019 | *Anisotoma humeralis* | | | | |
| K12 | Kelheim | 2019 | *Athous subfuscus* | | | | |
| K12 | Kelheim | 2019 | *Barypeithes tenex* | | | | |
| K12 | Kelheim | 2019 | *Epuraea pygmaea* | | | | |
| K12 | Kelheim | 2019 | *Euconnus pragensis* | 3 | | UE | |
| K12 | Kelheim | 2019 | *Lordithon lunulatus* | | | | |
| K12 | Kelheim | 2019 | *Malthodes fuscus* | | | | |
| K12 | Kelheim | 2019 | *Malthodes guttifer* | | | | |
| K12 | Kelheim | 2019 | *Melanotus rufipes* | | | | |
| K12 | Kelheim | 2019 | *Orthoperus mundus* | | | | |
| K12 | Kelheim | 2019 | *Orthoperus nigrescens* | 2 | | DD | |
| K12 | Kelheim | 2019 | *Oxypoda alternans* | | | | |
| K12 | Kelheim | 2019 | *Pteryx suturalis* | | | | |
| K12 | Kelheim | 2019 | *Quedius mesomelinus* | | | | |
| K12 | Kelheim | 2019 | *Rhinomias forticornis* | | | | |
| K12 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K12 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K13 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K13 | Kelheim | 2019 | *Echinodera hypocrita* | | | | |
| K13 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K13 | Kelheim | 2019 | *Orthoperus nigrescens* | 2 | | DD | |
| K13 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K13 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K14 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K14 | Kelheim | 2019 | *Anisoxya fuscula* | 3 | | | |
| K14 | Kelheim | 2019 | *Arthrolips obscurus* | 2 | | DD | |
| K14 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K14 | Kelheim | 2019 | *Haploglossa villosula* | | | | |
| K14 | Kelheim | 2019 | *Placusa pumilio* | | | | |
| K14 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K14 | Kelheim | 2019 | *Quedius cruentus* | | | | |
| K14 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K14 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K14 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K15 | Kelheim | 2019 | *Abraeus perpusillus* | | | | |
| K15 | Kelheim | 2019 | *Anaspis ruficollis* | 2 | 2 | | |
| K15 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K16 | Kelheim | 2019 | *Allecula rhenana* | 2 | | 2 | yes |
| K16 | Kelheim | 2019 | *Cryptophagus micaceus* | 2 | | | |
| K16 | Kelheim | 2019 | *Prionocyphon serricornis* | 3 | | UE | |
| K16 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K16 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K16 | Kelheim | 2019 | *Trixagus dermestoides* | | | | |
| K16 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K17 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K17 | Kelheim | 2019 | *Aulonothroscus brevicollis* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K17 | Kelheim | 2019 | *Quedius mesomelinus* | | | | |
| K17 | Kelheim | 2019 | *Rhizophagus bipustulatus* | | | | |
| K17 | Kelheim | 2019 | *Rhizophagus dispar* | | | | |
| K17 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K19 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K19 | Kelheim | 2019 | *Cryptophagus dentatus* | | | | |
| K19 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K19 | Kelheim | 2019 | *Placusa atrata* | | | | |
| K19 | Kelheim | 2019 | *Placusa pumilio* | | | | |
| K19 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K19 | Kelheim | 2019 | *Quedius cruentus* | | | | |
| K19 | Kelheim | 2019 | *Rhizophagus bipustulatus* | | | | |
| K19 | Kelheim | 2019 | *Thanasimus formicarius* | | | | |
| K19 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K19 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K19 | Kelheim | 2019 | *Xyloterus domesticus* | | | | |
| K20 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K20 | Kelheim | 2019 | *Anaspis flava* | | | | |
| K20 | Kelheim | 2019 | *Anaspis marginicollis* | | 2 | DD | |
| K20 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K20 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K20 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K24 | Kelheim | 2019 | *Dienerella clathrata* | | | | |
| K24 | Kelheim | 2019 | *Dienerella elongata* | | | | |
| K24 | Kelheim | 2019 | *Orthoperus nigrescens* | 2 | | DD | |
| K24 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K24 | Kelheim | 2019 | *Ptinella aptera* | | | | |
| K24 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K26 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K26 | Kelheim | 2019 | *Pityophagus ferrugineus* | | | | |
| K26 | Kelheim | 2019 | *Ptilinus pectinicornis* | | | | |
| K26 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K26 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K26 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K27 | Kelheim | 2019 | *Orthoperus nigrescens* | 2 | | DD | |
| K27 | Kelheim | 2019 | *Rhizophagus bipustulatus* | | | | |
| K27 | Kelheim | 2019 | *Scraptia fuscula* | 3 | 3 | | |
| K27 | Kelheim | 2019 | *Thanasimus formicarius* | | | | |
| K27 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K27 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K28 | Kelheim | 2019 | *Haploglossa villosula* | | | | |
| K28 | Kelheim | 2019 | *Orthoperus atomus* | | | | |
| K32 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K32 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K33 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K33 | Kelheim | 2019 | *Euplectus nanus* | | | | |
| K33 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K33 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K33 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K33 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K35 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K35 | Kelheim | 2019 | *Cryptophagus micaceus* | 2 | | | |
| K35 | Kelheim | 2019 | *Melanotus rufipes* | | | | |
| K35 | Kelheim | 2019 | *Prionocyphon serricornis* | 3 | | UE | |
| K35 | Kelheim | 2019 | *Quedius xanthopus* | | | | |
| K35 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K35 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K36 | Kelheim | 2019 | *Anaspis marginicollis* | | 2 | DD | |
| K36 | Kelheim | 2019 | *Anthribus albinus* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K36 | Kelheim | 2019 | *Corticaria longicollis* | | | | |
| K36 | Kelheim | 2019 | *Cryptophagus micaceus* | 2 | | | |
| K36 | Kelheim | 2019 | *Malthinus frontalis* | | | | |
| K36 | Kelheim | 2019 | *Melanotus rufipes* | | | | |
| K36 | Kelheim | 2019 | *Orthoperus mundus* | | | | |
| K36 | Kelheim | 2019 | *Orthoperus nigrescens* | 2 | | DD | |
| K36 | Kelheim | 2019 | *Prionocyphon serricornis* | 3 | | UE | |
| K36 | Kelheim | 2019 | *Quedius xanthopus* | | | | |
| K36 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K36 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K36 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K36 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K37 | Kelheim | 2019 | *Aleochara stichai* | | | | |
| K37 | Kelheim | 2019 | *Anaspis marginicollis* | | 2 | DD | |
| K37 | Kelheim | 2019 | *Anaspis ruficollis* | 2 | 2 | | |
| K37 | Kelheim | 2019 | *Atheta britanniae* | | | | |
| K37 | Kelheim | 2019 | *Cerylon histeroides* | | | | |
| K37 | Kelheim | 2019 | *Corticaria longicollis* | | | | |
| K37 | Kelheim | 2019 | *Cryptophagus micaceus* | 2 | | | |
| K37 | Kelheim | 2019 | *Echinodera hypocrita* | | | | |
| K37 | Kelheim | 2019 | *Malthodes sp.* | | | | |
| K37 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K37 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K37 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K38 | Kelheim | 2019 | *Aleochara stichai* | | | | |
| K38 | Kelheim | 2019 | *Alosterna tabacicolor* | | | | |
| K38 | Kelheim | 2019 | *Melanotus castanipes* | | | | |
| K38 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K38 | Kelheim | 2019 | *Prionychus melanarius* | 1 | | 2 | yes |
| K38 | Kelheim | 2019 | *Scaphisoma agaricinum* | | | | |
| K38 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K38 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K38 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K41 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K41 | Kelheim | 2019 | *Epuraea variegata* | | | | |
| K41 | Kelheim | 2019 | *Phloeostiba plana* | | | | |
| K41 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K41 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K42 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K42 | Kelheim | 2019 | *Anaspis flava* | | | | |
| K42 | Kelheim | 2019 | *Microscydmus minimus* | 3 | | | |
| K42 | Kelheim | 2019 | *Mycetochara linearis* | | | | |
| K42 | Kelheim | 2019 | *Mycetophagus populi* | 2 | 2 | 3 | |
| K42 | Kelheim | 2019 | *Neuraphes carinatus* | | | NT | |
| K42 | Kelheim | 2019 | *Phloeostiba lapponica* | | | | |
| K42 | Kelheim | 2019 | *Ptilinus pectinicornis* | | | | |
| K42 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K42 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K42 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K42 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K44 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K44 | Kelheim | 2019 | *Prionocyphon serricornis* | 3 | | UE | |
| K44 | Kelheim | 2019 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| K44 | Kelheim | 2019 | *Quedius invreae* | 3 | | | |
| K44 | Kelheim | 2019 | *Quedius truncicola* | 3 | | NT | yes |
| K45 | Kelheim | 2019 | *Aleochara sanguinea* | | | | |
| K45 | Kelheim | 2019 | *Gnathoncus buyssoni* | | | | |
| K45 | Kelheim | 2019 | *Hapalaraea pygmaea* | 3 | 3 | | |
| K45 | Kelheim | 2019 | *Mycetochara axillaris* | 2 | 2 | 2 | yes |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K45 | Kelheim | 2019 | *Mycetochara linearis* | | | | |
| K45 | Kelheim | 2019 | *Paromalus flavicornis* | | | | |
| K45 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K45 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K45 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K46 | Kelheim | 2019 | *Abraeus perpusillus* | | | | |
| K46 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K46 | Kelheim | 2019 | *Mycetophagus quadriguttatus* | | | | |
| K48 | Kelheim | 2019 | *Allecula rhenana* | 2 | | 2 | yes |
| K48 | Kelheim | 2019 | *Alosterna tabacicolor* | | | | |
| K48 | Kelheim | 2019 | *Ampedus pomorum* | | | | |
| K48 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K48 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K48 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K51 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K51 | Kelheim | 2019 | *Allecula rhenana* | 2 | | 2 | yes |
| K51 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K51 | Kelheim | 2019 | *Melanotus rufipes* | | | | |
| K51 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K51 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K52 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K52 | Kelheim | 2019 | *Aleochara stichai* | | | | |
| K52 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K52 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K52 | Kelheim | 2019 | *Malthodes marginatus* | | | | |
| K52 | Kelheim | 2019 | *Mycetochara linearis* | | | | |
| K52 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K52 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K52 | Kelheim | 2019 | *Xyloterus domesticus* | | | | |
| K58 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K58 | Kelheim | 2019 | *Anaspis rufilabris* | | | | |
| K58 | Kelheim | 2019 | *Atheta nigricornis* | | | | |
| K58 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K58 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K61 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K61 | Kelheim | 2019 | *Ampedus pomorum* | | | | |
| K61 | Kelheim | 2019 | *Hypebaeus flavipes* | 3 | 3 | 3 | |
| K61 | Kelheim | 2019 | *Mycetochara axillaris* | 2 | 2 | 2 | yes |
| K61 | Kelheim | 2019 | *Phloeophagus lignarius* | | | NT | |
| K61 | Kelheim | 2019 | *Rhamnusium bicolor* | 2 | 2 | 2 | yes |
| K61 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K61 | Kelheim | 2019 | *Stereocorynes truncorum* | | | | |
| K61 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K61 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K67 | Kelheim | 2019 | *Anaspis ruficollis* | 2 | 2 | | |
| K67 | Kelheim | 2019 | *Atheta nigricornis* | | | | |
| K67 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K67 | Kelheim | 2019 | *Melanotus castanipes* | | | | |
| K67 | Kelheim | 2019 | *Mycetophagus populi* | 2 | 2 | 3 | |
| K67 | Kelheim | 2019 | *Quedius brevicornis* | 3 | 3 | | yes |
| K67 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K67 | Kelheim | 2019 | *Trinodes hirtus* | 3 | | | |
| K67 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K68 | Kelheim | 2019 | *Corymbia scutellata* | | 2 | 3 | |
| K68 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K68 | Kelheim | 2019 | *Euplectus nanus* | | | | |
| K68 | Kelheim | 2019 | *Litargus connexus* | | | | |
| K68 | Kelheim | 2019 | *Mycetophagus quadripustulatus* | | | | |
| K68 | Kelheim | 2019 | *Placusa pumilio* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K68 | Kelheim | 2019 | *Tomoxia bucephala* | | | | |
| K68 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K68 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K68 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K69 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K69 | Kelheim | 2019 | *Denticollis linearis* | | | | |
| K69 | Kelheim | 2019 | *Pediacus depressus* | | | | |
| K69 | Kelheim | 2019 | *Phloeostiba plana* | | | | |
| K69 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K69 | Kelheim | 2019 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| K69 | Kelheim | 2019 | *Quedius truncicola* | 3 | | NT | yes |
| K69 | Kelheim | 2019 | *Rhizophagus bipustulatus* | | | | |
| K69 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K69 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K69 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K69 | Kelheim | 2019 | *Xyloterus signatus* | | | | |
| K70 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K70 | Kelheim | 2019 | *Atheta nigricornis* | | | | |
| K70 | Kelheim | 2019 | *Corticarina obfuscata* | 2 | 2 | DD | |
| K70 | Kelheim | 2019 | *Cryptolestes ferrugineus* | | | | |
| K70 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K70 | Kelheim | 2019 | *Melanotus castanipes* | | | | |
| K70 | Kelheim | 2019 | *Phloeonomus minimus* | 2 | 3 | | |
| K70 | Kelheim | 2019 | *Phloeostiba plana* | | | | |
| K70 | Kelheim | 2019 | *Placusa pumilio* | | | | |
| K70 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K70 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K70 | Kelheim | 2019 | *Xyloterus signatus* | | | | |
| K71 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K71 | Kelheim | 2019 | *Dienerella clathrata* | | | | |
| K71 | Kelheim | 2019 | *Dienerella elongata* | | | | |
| K71 | Kelheim | 2019 | *Eucnemis capucina* | 3 | 3 | 3 | yes |
| K71 | Kelheim | 2019 | *Haploglossa villosula* | | | | |
| K71 | Kelheim | 2019 | *Orthoperus mundus* | | | | |
| K71 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K71 | Kelheim | 2019 | *Rhizophagus bipustulatus* | | | | |
| K71 | Kelheim | 2019 | *Thamiaraea cinnamomea* | 3 | | | |
| K71 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K71 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K71 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K72 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K72 | Kelheim | 2019 | *Atheta nigricornis* | | | | |
| K72 | Kelheim | 2019 | *Placusa atrata* | | | | |
| K72 | Kelheim | 2019 | *Placusa tachyporoides* | | | | |
| K72 | Kelheim | 2019 | *Quedius mesomelinus* | | | | |
| K72 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K73 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K73 | Kelheim | 2019 | *Prionocyphon serricornis* | 3 | | UE | |
| K73 | Kelheim | 2019 | *Xyleborus peregrinus* | | | | |
| K73 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K74 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K74 | Kelheim | 2019 | *Epuraea neglecta* | | | | |
| K74 | Kelheim | 2019 | *Litargus connexus* | | | | |
| K74 | Kelheim | 2019 | *Mycetophagus quadripustulatus* | | | | |
| K74 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K74 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K74 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |
| K75 | Kelheim | 2019 | *Aleochara sparsa* | | | | |
| K75 | Kelheim | 2019 | *Aleochara stichai* | | | | |

| ID | Study region | Year | Species | Red List of Germany (1998) | Red List of Bavaria (2005) | Red List of Germany (2021) | Tree hollow specialist species |
|---|---|---|---|---|---|---|---|
| K75 | Kelheim | 2019 | *Dienerella clathrata* | | | | |
| K75 | Kelheim | 2019 | *Dienerella elongata* | | | | |
| K75 | Kelheim | 2019 | *Placusa pumilio* | | | | |
| K75 | Kelheim | 2019 | *Ptenidium gressneri* | 3 | 3 | 3 | yes |
| K75 | Kelheim | 2019 | *Sericoderus lateralis* | | | | |
| K75 | Kelheim | 2019 | *Stenomax aeneus* | | | NT | |
| K75 | Kelheim | 2019 | *Xyleborus dispar* | | | | |
| K75 | Kelheim | 2019 | *Xyleborus germanus* | | | | |
| K75 | Kelheim | 2019 | *Xyleborus saxeseni* | | | | |

## (Eidesstattliche) Versicherungen und Erklärungen

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

*Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 97 Abs. 1 Satz 8 BayHIG).*

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

*Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.*

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*Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.*

(§ 9 Satz 2 Nr. 7 PromO BayNAT)

*Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.*

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