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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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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

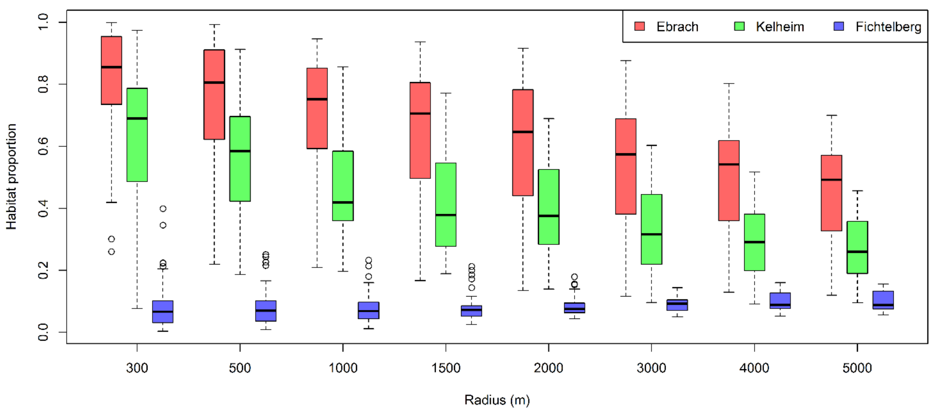

Fig. 1 Habitat proportion (i.e., proportion of deciduous forest) surrounding the focal tree hollows at radii of 300–5000 m in the three forest regions Ebrach, Fichtelberg, and Kelheim in Bavaria (Germany). Ebrach: $n = 50$ tree hollows, Fichtelberg: $n = 43$, Kelheim: $n = 41$

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).

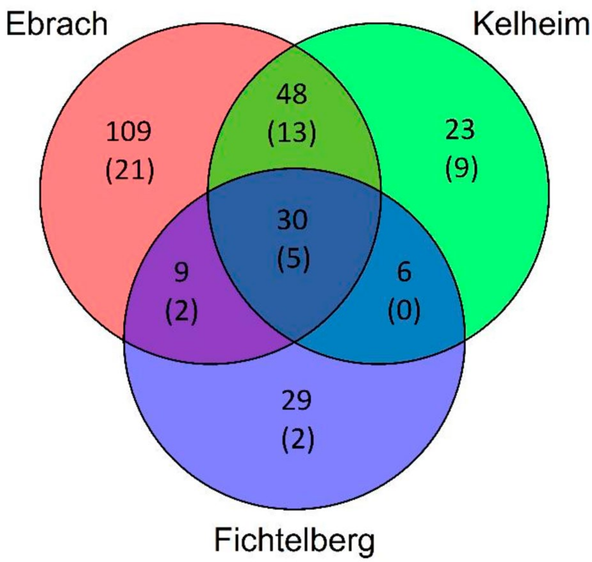

Fig. 2 Venn diagram comparing the saproxylic beetle species richness (threatened species richness) and species composition in the three forest regions in Bavaria, Germany. Ebrach: 196 species (41 threatened species) ($n=50$ tree hollows), Fichtelberg: 74 species (9 threatened species) ($n=43$), Kelheim: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

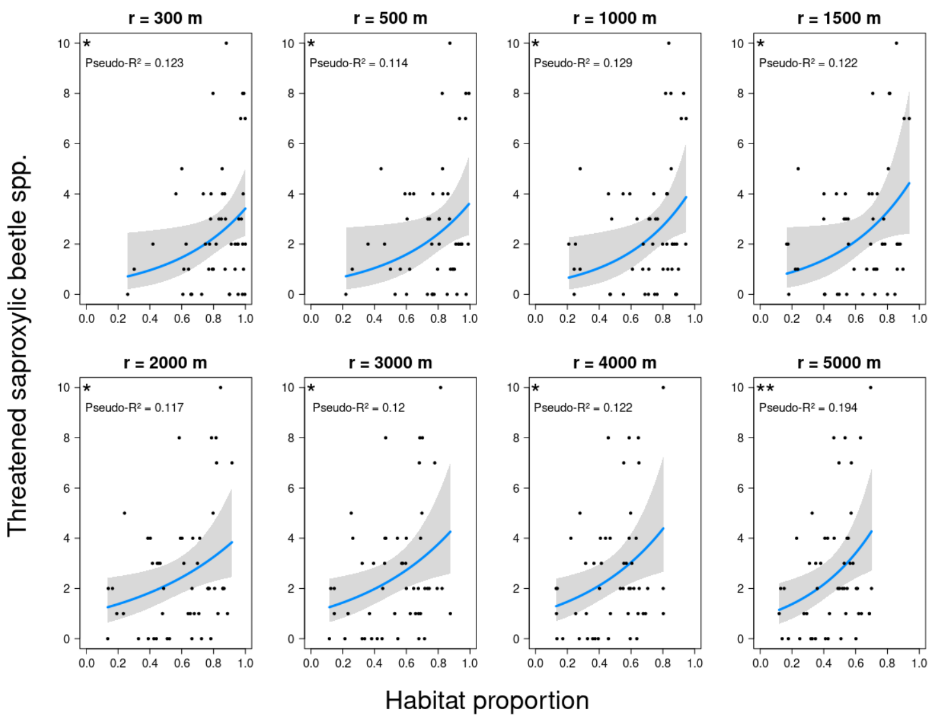

Fig. 3 GLMs of the Ebrach forest management district. Species richness of threatened saproxylic beetles as dependent variable; habitat proportion at different radii around the focal tree hollows (n = 50) as explanatory variable. p < 0.05 (*), p < 0.01 (**). Pseudo-² values show the explanatory power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

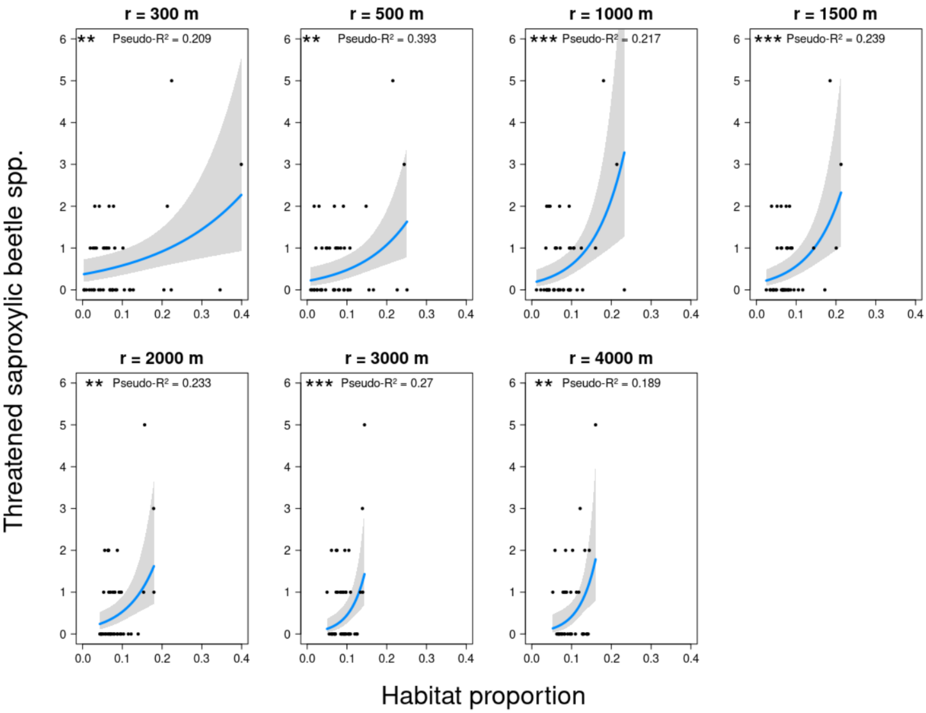

Fig. 4 GLMs of the Fichtelberg forest management district. Species richness of threatened saproxylic beetles as dependent variable; habitat proportion at different radii around the focal tree hollows ($n=43$) as explanatory variable. $P<0.01$ (**), $p<0.001$ (***). Pseudo-R^2 values show the explanatory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

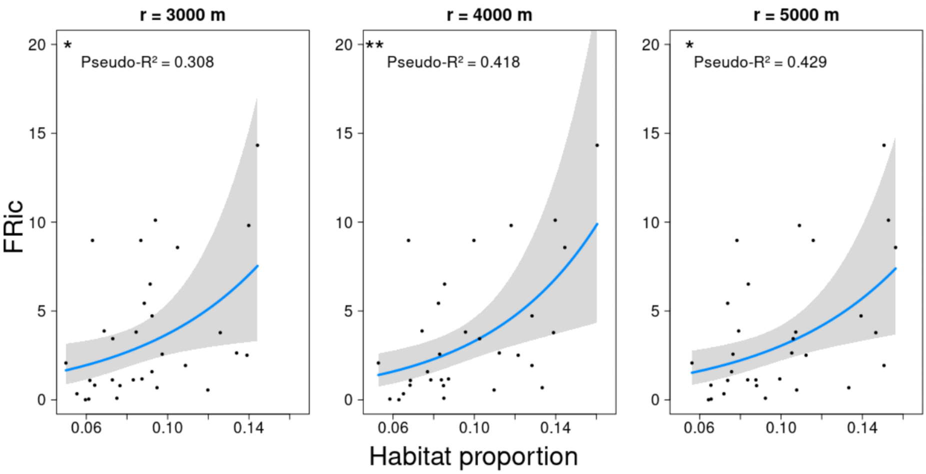

Fig. 5 GLMs of the Fichtelberg forest management district. Functional richness (FRic) of saproxylic beetles as dependent variable; habitat proportion at radii of 3000 m, 4000 m, and 5000 m around the focal tree hollows ($n=43$) as explanatory variable. $p<0.05$ (*), $p<0.01$ (**). Pseudo-R² values show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

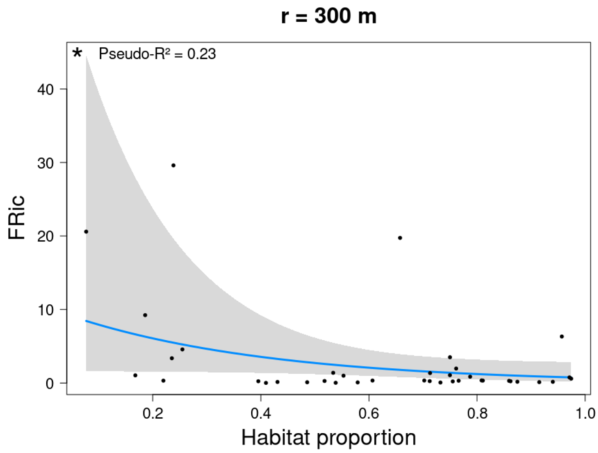

Fig. 6 GLM of the Kelheim forest management district. Functional richness (FRic) of saproxylic beetles as dependent variable; habitat proportion at a radius of 300 m around the focal tree hollows ($n=41$) as explanatory variable. $p<0.05$ (*). The pseudo-R² value shows the explanatory power of the model

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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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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