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Congruence of biodiversity patterns between woodland associated Hymenoptera and saproxylic Coleoptera

Ph.D. Thesis

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Annotation

This thesis consists of four studies, focusing on the diversity of aculeate Hymenoptera in various woodland environments, which were affected by various disturbance agents and management regimes. We assessed the effect of deadwood retention and salvage logging on communities of woodland bees and wasps after windthrows and also the diversity and composition of nesting communities of saproxylic bees and wasps in woody steppe and neighbouring shady forest.

Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

In České Budějovice,

20.5.2024 Michal Perlík

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List of publications and author's contribution

The thesis is based on the following publications:

I. Georgiev, K.B., Beudert, B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., **Perlík, M.**, Weiss, I. and Thorn, S. (2021) 'Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity', Forest Ecology and Management, 495(May), p. 119354. https://doi.org/10.1016/j.foreco.2021.119354.
MP identified the Hymenoptera samples for the study and took part in writing and revising the manuscript. His contribution was 10%.

II. Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., **Perlík, M.**, Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Żmihorski, M. and Leverkus, A.B. (2020) 'Estimating retention benchmarks for salvage logging to protect biodiversity', *Nature Communications*, 11(1), p. 4762. https://doi.org/10.1038/s41467-020-18612-4.
MP identified the Hymenoptera samples, compiled the Hymenoptera traits and took part in revising the manuscript. His contribution was 10%.

III. **Perlík, M.**, Kraus, D., Bußler, H., Neudam, L., Pietsch, S., Mergner, U., Seidel, D., Sebek, P. and Thorn, S. (2023) 'Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging', *Forest Ecology and Management*, 540, p. 121033. https://doi.org/10.1016/j.foreco.2023.121033.
MP took part in fieldwork, identified the Hymenoptera samples, compiled the Hymenoptera traits, took part in the data analysis, wrote the first draft and revised the manuscript after reviews. His contribution was 60%.

IV. **Perlik, M.**, Ambrozova, L., Jirku, D., Jirku, M. and Sebek, P. (2024) 'Microbiotope selection in saproxylic bees and wasps (Hymenoptera, Aculeata): cavity-nesting communities in forests and wooded pastures are affected by variation in openness but not deadwood', *Journal of Insect Conservation*, 28(2), pp. 269–282. https://doi.org/10.1007/s10841-023-00545-0.
MP designed the study, did all fieldwork and rearing, identified the reared specimens, analysed the data, wrote the first draft and revised the manuscript after reviews. His contribution was 80%.

Co-author agreement:

Pavel Šebek, the supervisor of the Ph.D. thesis and co-author of the publications "Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging" and "Microbiotope selection in saproxylic bees and wasps (Hymenoptera, Aculeata): cavity-nesting communities in forests and wooded pastures are affected by variation in openness but not deadwood," fully acknowledges the stated contribution of Michal Perlík to the publications.

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Kostadin B. Georgiev, the lead author of the publication "Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity" and co-author of the publication "Estimating retention benchmarks for salvage logging to protect biodiversity," fully acknowledges the stated contribution of Michal Perlík to the publications.

Kostadin B. Georgiev..

Simon Thorn, the lead author of the publication "Estimating retention benchmarks for salvage logging to protect biodiversity" and co-author of the publication "Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging," fully acknowledges the stated contribution of Michal Perlík to the publications.

Simon Thorn..

Contents

Introduction

Introduction

1. European woodlands

1.1. Distribution and composition

Woodlands are any type of environment involving woody plants, i.e. trees and shrubs, predominantly woods or forests. The forests account for over 35% of European area (EEA, 2020; FAO, 2022). Proportional cover of forests is not uniform among countries, with higher forest cover being present in the north (Baltic countries and Fennoscandia) and lower in central Europe (Kuuluvainen and Aakala, 2011). Similarly, the age and tree species composition is regionally variable. On average, three quarters of all forests are even-aged stands, almost half of all European forests are conifer dominated, more than a third of forests are broadleaf stands and around 17% are mixed stands. Conifer dominated forests are more widespread in the north and in higher altitudes, while broadleaf forests are typical for low and middle elevations and southern latitudes. Large proportion, over 76%, of forests are available for wood and timber extraction of any kind. Many of these are production forests, i.e. grown and managed for the main purpose of wood and timber production, often they are also planted. More than one third of all European forests are single species stands (Kraus and Krumm, 2013; Rigo et al., 2016; FAO, 2022). Almost a third of forests are protective forests, which means they serve to stabilize their environment, mostly to prevent soil erosion (FAO, 2022). Lastly, about a quarter of all European forests are protected for purposes of nature conservation (Muys et al., 2022). However, the above mentioned categories of forests are not exclusive and even many protected forests are subject to some degree of logging or are also considered protective.

The woodland and forest habitats host vast variety of associated organisms. Such organisms often depend on trees or shrubs, wood, deadwood or their associated microhabitats or on other woodland organisms such as fungi, specialist plants or prey (Fayt et al., 2006; Timonen et al., 2010; Lassauce et al., 2011; Proctor et al., 2012; Hagge et al., 2019). Diversity and population dynamics of forest associated organisms are affected by local and regional forest structure. Such structure can be measured at local scale, as local openness or as vertical stratification, or at larger scale, as a distribution of various forest types. Canopy openness, i.e. the degree to which the crowns of trees and shrubs allow sunlight to reach lower forest strata, is a particularly important factor which affects local microclimate (Ehbrecht et al., 2019; Horváth et al., 2023). Microclimate strongly affects humidity, development rates of ectotherm organisms and decay rate of the dead biomass under forest canopy (Rackham, 2008; Magrach et al., 2012; Müller et all., 2020; De Frenne et al., 2021). Forest structure is usually not homogeneous over larger areas, instead, it is determined by properties of soil, climatic conditions, geographic constraints, and to a large degree by forest successional stage and disturbance events.

1.2. Structure and dynamics

Through the course of succession, the forest habitat structure changes profoundly. The early-successional forest stages of forests have high canopy openness and low vegetation cover. At the same time there may be little to no deadwood if the early-successional stage formed as result of logging, which removes timber and hence deadwood. Otherwise, the deadwood is left on site and subject to decay (Kupfer and Runkle, 1996; Hilmers et al., 2018; Kovac, Hladnik and Kutnar, 2018). After the early stage of succession, the forests turn into regenerating and later mature stage, which is typical by dense growth, high canopy cover, shade tolerant forest floor vegetation and overall moister microclimate. Without a disturbance, be it natural or man-made, forests remain shady and relatively uniform for an unspecified period of time in a “climax-like” state, with low variation in deadwood qualities as well as microclimates. Mature forests have long been considered the stable climax of local vegetation succession (Petrokas, 2020), however that is only true for systems where major disturbance agents are absent. Late successional stages of forest succession typically have more accumulated deadwood, higher canopy openness and overall warmer microclimate (Hilmers et al., 2018). Here, it is worth noting that succession is a cyclic system and so the late, dying and senescent stages are followed by early, open and regenerating stages (Hilmers et al., 2018). Deadwood within forest environments is vital resource for a group of saproxylic (deadwood dependent) organisms (Jansen et al., 2020; EEA, 2020; Müller et al., 2020). However, just high amount of deadwood does not necessarily increase biodiversity, but rather diversity of decay classes, sizes, types, and orientations (standing, grounded) benefits deadwood dependent biodiversity past certain volume thresholds (Lassauce et al., 2011; Lachat et al., 2012; Milberg et al., 2016; Thorn et al., 2016; Rubene, Schroeder and Ranius, 2017; Doerfler et al., 2020; Neff et all., 2022). Deadwood microhabitats such as tree hollows, fungal fruiting bodies, are vital for saproxylic organisms (Bouget et al., 2014). Also, different tree species produce different qualities of deadwood depending on local microclimate and these can attract specialized organisms (Speight, 1989; Lassauce et al., 2016; Lachat et al., 2016; Eckerter et al., 2021).

Heterogeneity of woodland and forest environments depends on occurrence of disturbances at various spatial scales and with various severity (Angelstam and Kuuluvainen, 2004; Stevens et al., 2015; Heikkala et al., 2016; Weiss et al., 2021). Historically, natural disturbances such as windthrows, forest fires, insect gradations, floods, landslides or large herbivore grazing were responsible for altering the successional pathways or effectively resetting the local habitat to its earlier successional stage. While many natural disturbance agents have been suppressed from modern landscapes, many management practices can substitute them and render similar service to the ecosystem (Proctor et al. 2012; Feurdean et al., 2017; Burton et al., 2020). They can, however, be so intensive, that they do not leave any remnants of previous habitat, e.g. heavy habitat modification typical for logging and wood harvest. The remnants of previous habitats are called biological legacies and include various deadwood items (logs, stumps, coarse woody debris), solitary trees, bare soil, etc. Legacies then serve as stepping stones for specialized organisms of the disturbed sites as well as a feature connecting the remnants of the former habitat to the modified, disturbed one (Rudolphi, Jönsson and Gustafsson, 2014; Zolotarjova, Kraut and Lõhmus, 2016; Augustynczik et al., 2020). Disturbances occur on many spatial and temporal scales which have differing effects on the forest habitats. While small scale disturbances (such as tree fall gaps) also modify local microclimate, they are often too small to considerably change the surrounding habitat (Bouget and Duelli, 2004; Zolotarjova, Kraut and Lõhmus, 2016). Furthermore, small, disturbed habitats can succumb to succession fairly fast, so they only create open habitats for short time period (Kupfer et al., 1996; Kozel et al., 2021; Weiss et al., 2021). Because of this, small scale disturbances are only able to structure forest environments when they are sufficiently frequent over large area (McCarthy, 2001; Lachat et al., 2016). More severe or large disturbance events create more pronounced and long-term habitat modification towards open conditions. The frequency at which disturbances occur together with the size of affected area are vital for establishment of heterogeneous forest landscape mosaic with high multifunctionality (Burton, Jentsch and Walker, 2020; Markgraf et al., 2020; Heidrich et al., 2023; Rappa et al., 2024).

1.3. Woodland biodiversity

Biodiversity of forest associated organisms is closely associated with the heterogeneity of forest structure, disturbance dynamics and distribution of various successional stages in space and time. Open stages of forest succession often host different species composition than advanced stages or mature forest stands, late-successional stages can have specific deadwood properties, etc. (Sebek et al., 2016; Hilmers et al., 2018; Kozel et al., 2021). But biodiversity itself has many facets and these are scale dependent (Whittaker, 1972; Andremann et al., 2022). Alfa diversity describes species diversity (richness) on a local scale (patch of forest, forest clearing, meadow, etc.), within a functional community. Beta diversity is differentiation of communities among local sites, or absolute species turnover among sites. Compared to alpha diversity, it is a more complicated concept, which is used differently depending on context. Generally though, beta diversity refers to dissimilarity in species composition between sites (Sørensen dissimilarity, Jaccard index, inverse Morisita-Horn index etc.) or, more traditionally as the ratio between local (alpha) and regional (gamma) diversity. It is worth noting, that two sites with low alpha diversity can have high beta diversity between them if they represent largely different communities (Tuomisto, 2010a; Tuomisto, 2010b). Lastly, gamma diversity refers to diversity at larger scales, often regional. In this way it is the cumulative number of species across an area. Checklists of species and large scale faunistic or floristic studies often operate with gamma diversity, whereas in experimental studies comparing different habitats or microbiotopes within a particular forest, alfa and beta diversity are of primary interest. For forest environments, the aforementioned heterogeneous structure may not necessarily increase local alpha diversity but instead drive high beta diversity and subsequently gamma diversity in the whole study system. In homogeneous forest stands, where disturbances do not diversify the structure, alpha diversity can be comparable to more heterogeneous stands but beta diversity, i.e. differentiation among communities, can be low, which potentially leads to impoverished forest biodiversity at landscape level (Tylianakis et al., 2006, but see also Schall et al. 2020). It is hence important to always consider the effect of forest structure and its habitats on woodland biodiversity at multiple scales including the temporal ones. If the forest succession and disturbance dynamics are largely absent, the forest usually remains homogeneously shady for a long time period creating low temporal beta and even alpha diversity depending on the observed time period (Magurran et al., 2019). The various measures of biodiversity are used to assess biological value of woodland and forest habitats across scales as well as to describe changes in the communities inhabiting such habitats.

1.4. Woodland biodiversity conservation

Problems arise, when biodiversity conservation comes into play as many forests serve primarily a production function (EEA, 2020). There are two main approaches to forest conservation: integrative and segregative (Blattert et al., 2018). Segregative approaches typically designate selected areas for conservation, which are usually considered biologically valuable based on locally relevant concept or indicators of diversity, and removes them from production forest management (Bouget et al., 2014). Such approaches typically create larger or smaller islands of protected areas in the matrix of, unprotected production forests. Here, the ways the biological values and processes are "protected" in such forests also differ depending on tradition, law, precedent state or resources of local managers. The protection measures can include active management actions, aiming to supply the disturbance pressure increasing heterogeneity at various scales within these protected areas (Franc and Götmark, 2008; Sjödin, Bengtsson and Ekborn, 2008; Sebek et al., 2015; Kovac, Hladnik and Kutnar, 2017; Doerfler et al. 2020). Alternatively, some protected areas employ a "hands off" approach, limiting human intervention to the environment and relying strictly on spontaneously occurring natural processes. This approach, however, requires local natural disturbance processes to be preserved for the environment to support heterogeneous habitats and associated biodiversity (Hilmers et al., 2018; Franc and Götmark, 2008). Without disturbances the protected areas tend to remain in a stable state resembling the concept of climax communities, i.e. with prevailing high canopy closure and shading and lack of larger open habitats, which in turn can lead to impoverishment of biodiversity (Spitzer et al., 2008; Bouget et al.,2014; Miklín and Čížek, 2014; Miklín et al., 2017). The approach can be especially detrimental if it is applied in areas where the biological value was derived from former managements or disturbance regimes (Hédl, Kopecký and Komárek, 2010; Müllerová, Hédl and Szabó, 2015; Sebek et al., 2015). Alternatively, some authors refer to wild, large herbivore pastures as hands off approach as well. This is only true for pasture regimes where large herbivores are introduced and, ideally, left mostly unmanaged, i.e. rewilding. However, as with any other systems, correct densities and grazing pressure in limited areas need to be managed in order to prevent unnecessary damage to froest habitats (Vera, 2000; Dandy and Wynne-Jones, 2019; Konvička et al., 2021).

Compared to the mentioned segregative approach, integrative approach aims to implement specific conservation measures into different types of forests while maintaining the principal function for human society – wood and timber supply. Planting and management in such areas aims to balance production in homogeneous blocks, vital for logging effectivity, with disturbances and natural development of legacies and microhabitats, which increase system resilience and biodiversity (Kraus and Krumm, 2013; Mann et al., 2018; Kuuluvainen et al., 2021; Zumr, Remeš and Pulkrab, 2021). Here, properly planned handling of logging operations at various scales can considerably benefit biodiversity. Retention of some large living, or dead trees, as well as deadwood legacies during logging mitigates the negative outcomes of logging itself (Pengelly and Cartar, 2010; Koch Widerberg et al., 2012; Walters et al., 2016; Zolotarjova, Kraut and Lõhmus, 2016; Leverkus et al., 2018; Leverkus et al., 2021). Integrative approaches do not need to be associated with planned forestry activites only. For instance, when spontaneous disturbances occur, many countries currently mandate "salvage logging" – salvaging some valuable timber after disturbance events. The salvage logging creates a disturbance cascade with the previous disturbance and may alter the course of future succession as well as lessen the ecosystems resistance to future disturbances. The integrative approach in this context is to carefully plan how much timber can be extracted during salvage logging and how much deadwood should be left at the site to foster biodiversity of organisms which can exploit it. It can be, however, sometimes hard to implement and legally challenging, depending on local policy (Thorn et al., 2018; Leverkus et al., 2021). Other integrative systems highlight the creation of small clearcuts in mosaics across spatial and temporal scales. The emulation of larger disturbances which increase canopy openness such as prescribed burning or traditional management practices such as coppicing have been found invaluable tools of woodland conservation efforts at many sites (Fartman, Müller and Poniatowski, 2013; Lettow et al., 2018; Schulze Rosenthal and Peringer, 2018). Integration of biodiversity conservation aspect to large areas of production forests may therefore increase all levels of diversity on landscape scale while still ensuring timber resources and other functions of woodlands.

Different features of forest habitats and different management approaches which shape them, affect organisms in different ways. Complex outlook is often necessary to support diverse communities of woodland associated organisms.

2. Woodland organisms

Woodland and saproxylic organisms are essential parts of their respective ecosystems and their habitat requirements and response of their communities to management can vastly differ. Many plant species are forest specialists, and their richness is affected by various forest management actions (Schulze, 2017). Additionally, many epiphytic but also epigeic lichens and bryophytes are associated with woodland habitats and are especially affected by the woodland continuity and air quality (Wulf, 2003; Whittet and Ellis, 2013). Various groups of fungi are vital for proper function of their respective ecosystems as they are prominent decomposers. They are also often in mutualistic or parasitic relationship with other organisms like woodland trees (Volk, 2013). Many saproxylic fungal species are substrate specific and also host distinct communities of fungivores (Jonsell et al., 1998; Thorn et al., 2015; Hagge et al., 2019; Haeler et al., 2021; Meyer, Rusterholz and Baur, 2021). Saproxylic fungi are therefore considered indicators of diversity of other saproxylic organisms, to which they serve as feeding substrate. Saproxylic beetles remain one of the best studied insect groups (Lassauce et al., 2011; Graf et al., 2013; Bouget et al., 2014; Miklín et al., 2018; Doerfler et al., 2020; Hagge et al., 2021) and serve as a model group in the context of forest biodiversity patterns. Current body of literature offers some insights into general underlying determinants which seem to be common to diversity of many organisms, ecological groups and forest habitat types. Generally, it is openness and variability of open structures, which alter local microclimate, and deadwood and its diversity, which are key aspects of substrate provision for the decomposing food chains (Koch Widerberg et al., 2012; Seibold et al., 2016; Zolotarjova, Kraut and Lõhmus, 2016; Müller et al., 2020).

However, beetles are, of course, only a part of insect biodiversity associated with forests and many other groups remain understudied. Many species of flies (Diptera) are saproxylic, but unlike beetles, many of them prefer moist rot wood and late wood decay stages (Fayt et al., 2006; Jonsell, Windenfalk and Hellqvisst, 2020). Many hemipteran groups (Pentatomorpha, Cimicomorpha, Aradimorpha, Dipsocomorpha etc.) include species which also inhabit woodlands and their deadwood. Many herbivorous species feed on living plants by sucking on phloem or xylem – such species also inhabit woodlands when suitable host plants are present. They can similarly feed on the hyphae of saproxylic fungi, and many are predators within deadwood. Saproxylic Hemiptera in Europe are, however, not very species rich (around 5000 species worldwide) and so they are usually not considered as vital for saproxylic biodiversity, with assumed ecological needs focusing around deadwood created by disturbances, and deadwood microhabitat diversity (Gossner and Damken, 2018). Bees and wasps also inhabit various woodland environments, but are less prominent in research (Taki et al., 2008; Sobek et al., 2009; Matsumoto and Makino, 2011; Rappa et., 2024). Many parasitic and parasitoid wasps use woodboring larvae, including those of beetles, as hosts or use beetle galleries in deadwood for nesting (Hilszczański, 2018). Deadwood nesting is common for many species of bees as well.

The main subject of the present thesis is the comparison of diversity between saproxylic beetles and woodland Hymenoptera, two woodland insect groups which are given unequal scientific attention, within various woodland environments. Both focal insect groups, their ecology, major differences and the implications for their conservation are described below.

3. Beetles

Beetles are well studied and diverse order of insects fulfilling a variety of ecological functions (Losey and Vaughan, 2006; McKenna et al., 2019; Basile et al., 2023). These include predation, nutrient cycling through decomposition and pathogen suppression via cadaver and dung removal (New, 2007; Barclay and Bouchard, 2023). With over 29000 species recognized worldwide, many ecosystems are strongly affected by their diversity (Calix et al., 2010). With high diversity and large number of species of ecological significance, saproxylic beetles are one of the best studied insect groups in context of woodland or forest ecology (Sebek et al., 2016; Eckelt et al., 2018; Hagge et al., 2021).

Saproxylic beetles are beetles that depend on deadwood, old and sensecent trees or deadwood microhabitats (cavities, crack, fruiting bodies of fungi, and others) during some part of their life cycle. The saproxylic beetles may depend on deadwood in various ways – they can use it as substrate for feeding, or as indirect resource such as substrate for fungi and molds which the beetles feed on, or they can be predators and use deadwood as hunting grounds (Hagge et al., 2019; Haeler et al., 2021; Meyer, Rusterholz and Baur, 2021). In Europe, there are more than 2600 described species (Bouget et al., 2019). However, their species richness in Europe is estimated to be close to 4000 species by some authors (Calix et al., 2010). Saproxylic beetles can be found in many families, diverse ones include Cerambycidae, Buprestidae, Elateridae, Lucanidae, Scarabeidae, Curculionidae, Mycetophagidae, or Tenebrionidae, but there also many other smaller, less conspicuous ones such as Mordellidae, Cucujidae, Erotylidae or Latridiidae among many others (Schmidl et al., 2004; Brin and Bouget, 2018). Because of their diversity and strong relation to woodland habitats, many are used as indicator species in ecological research; their presence in the local community indicates the state of the environment or presence of biologically valuable structures such as certain deadwood microhabitats (Brin and Bouget, 2018). Furthermore, the knowledge of the habitat requirements of several emblematic species allows to use them as flagship species of given communities. This concept is often used in nature conservation, where conservation effort focused on selected species, called umbrella species, benefits entire associated community and their habitat. In Europe, saproxylic beetles are often considered flagship species of old-growth forest, veteran trees or remnants of woodland pasture communities (Lachat et al., 2012; Naskrecki, 2013). Some of the saproxylic beetles are also considered ecosystem engineers, able to considerably affect their environment. Some of these species, in particular bark beetles (Scolytinae), are considered pests by some foresters as they may cause qualitative and economic damages in production stands (Bouget and Duelli, 2004; Křivan et al., 2016; Tsikas and Karanikola, 2022).

4. Bees and wasps

The order Hymenoptera is a species rich order including many species of pollinators, which, in modern landscapes, face serious decline and as such, the study of their ecological needs is more essential than ever (Losey and Vaughan, 2006; Gallai et al., 2009; Angelstam et al., 2013; Wardhaugh, 2015; Brock, Cini and Sumner, 2021). Besides pollinators, many species are predators and parasitoids, fulfilling important biological functions within their respective food webs (Hilszczański, 2018; Brock, Cini and Sumner, 2021). Aculeate Hymenoptera are a monophyletic subclade within Hymenoptera, where female ovipositor evolved into stinger (Michener, 2007). This group includes, among other less conspicuous groups, bees and wasps. Among most prominent aculeate features is their parental care and building of nests, which is fairly rare among insects (Radchenko, 1996; Gilbert and Manica, 2015; Field, Gonzalez-Voyer and Boulton, 2020). Bees and wasps are able to nest in various substrates (soil, wood, stems, snail shells, rock cavities etc.) below and above ground, or, in a very few cases, build nest structures of their own.

About 20% of European aculeate hymenopterans utilize various, mostly preexisting, cavities for nesting. These cavities may be of different origin, from cracks in bark, wood or rock, hollow stems, empty snail shells, galls, to beetle galleries in deadwood. Out of approximately 250 species of cavity nesters, more than 100 species nest in deadwood (including deadwood specialists and cavity generalists known to use also cavities in other substrates) (Macek et al., 2010; Bogusch and Horák, 2018). As such, they are vital part of the diversity of bees and wasps, and supporting management action which create environments rich with deadwood nesting opportunities aids not just this ecological group of insects, but others, like saproxylic beetles, as well.

Woodlands seem like a logical focal habitat for saproxylic cavity-nesting Hymenoptera to inhabit. Such habitats have trees and associated deadwood and deadwood microhabitats, which can be inhabited by woodboring insects, which create galleries, which, in turn, can serve as nesting cavities (Taki et al., 2008; Dufour-Pelletier et al., 2020; Urban-Mead et al., 2021). Deadwood management in anthropogenic landscapes is known to positively affect biodiversity of saproxylic organisms like cavity-nesters, provided that the deadwood items as well as microclimate vary sufficiently (Benes et al., 2006; Horak et al., 2014; Rudolphi, Jönsson and Gustafsson, 2014; Sebek et al., 2016; Siqueira et al., 2017). Furthermore, various forest management practices also structure the environment and create deadwood. Logging and even clearcutting creates stumps, damages surrounding woody vegetation, and often leaves fine and coarse woody debris (FWD, CWD) on site (Morato and Martins, 2006; Sobek et al., 2009). More traditional practices add to this in a way much closer resembling natural processes. While broader structure of woodland/forest, along with the nesting resource availability definitely play a role in structuring the communities of cavity-nesters, the surrounding habitats and the availability of feeding/foraging patches are just as vital. Places where flowering plants and/or prey are abundant throughout the vegetation season are as important as nesting opportunities. The nesting and foraging ecological requirements both have to be met to allow the communities of cavity nesters to thrive (Hoehn, Steffan-Dewenter and Tscharntke, 2010; Schüepp et al., 2011; Fabian et al., 2013; Rubene, Schroeder and Ranius, 2015). Another important factor, which can potentially negatively affect the cavity-nesters, is use of commercial pesticides or insecticides on agricultural land in the vicinity of the nesting sites, foraging sites, or directly on them, even when relatively infrequent (Kevan, 1999; Douglas et al., 2022; Chreil and Maggi, 2023; Nicholson et al., 2023).

5. Comparison of focal insect groups

5.1. Habitat requirements

Saproxylic beetles and cavity-nesting woodland aculeate Hymenoptera share some ecological requirements, but they also differ considerably. While both insect groups depend on some form of deadwood for their development, their other life requirements strongly affect how they function in any given habitat. Contrary to saproxylic beetles, whose adults often feed and move between sites minimally, bees and wasps require foraging grounds within suitable foraging distance from nest site to be able to provide for their larvae in the nest (Gathmann and Tscharntke, 2002; Michener, 2007; Hedin et al., 2008; Lindman et al., 2020). Egg deposition by saproxylic beetles is conditioned by females being mated and finding a suitable deadwood item for the development of their larvae but does not require further investments from the parent (Gimmel and Ferro, 2018; Köhler et al., 2022). On the contrary, aculeate Hymenoptera lay their eggs into brood cells in the nest but at the same time they also must provide food provision for development of the larvae to-be, in particular pollen in case of bees and arthropod prey in case of wasps. This is time and energy consuming and so suitable habitat configuration with nesting and foraging patches is vital (Roberts and Krombein, 1967; Grundel et al., 2010; Hagen, Wikelski and Kissling, 2011; Torné-Noguera et al., 2014).

5.2. Larval feeding and life cycle

Because saproxylic beetle larvae feed on deadwood and its fungi, correct selection of deadwood item or microhabitat, local microclimate (often affected by vegetation structure), decay stage and tree species, is vital for their successful development. The life cycle of saproxylic beetles takes on average around two years, with differences among species largely based on body size – small species can have have even two or three generations per year whereas large species develop over several years, up to 4 or 5 years in the largest ones (Fremlin, 2022). During that time the larva is entirely dependent on the original parental choice of feeding substrate. If the substrate is depleted or the quality changes (the wood dries up, becomes too wet etc.) the larva might not be able to successfully develop. For some species deadwood item size plays and important role as such items have more stable microclimate but also can sustain large populations over longer period of time (Horak et al., 2014; Gimmel and Ferro, 2018; Haeler et al., 2021). Meanwhile adults od saproxylic beetles usually do not consume deadwood (occasionally they feed on sap, pollen or nectar or are predatory) (Buse, Ranius and Assmann, 2008; Bonacci et al., 2020). For larvae boring in wood or living under bark, the wood also serves as a form of protection from parasites and predators, as specialized behaviour is required from their enemies to locate and hunt these larvae. Such predators either destroy the wood to get to the larvae (woodpeckers), follow them in the wood galleries (Histeridae, Cleridae etc.), or are able to reach the larvae through the wood, usually via a long ovipositor (Ichneumonids, Braconids) (Dufour-Pelletier et al., 2020; Muys et al., 2022). Many natural enemies are also parasitoids of the saproxylic beetle pupas (Tachinidae, Orussidae) (Tscharntke et al., 2007; Henry and Roitberg, 2009). With most beetle adults being short-lived, the ecological needs of adults are secondary to the larval development requirements.

On the contrary, adult bees and wasps, while also short-lived, provide food for the larvae in their nest and so are more dependent on resources besides the nesting substrate. The life cycle of most saproxylic aculeate Hymenoptera species takes one year or less, with many species having several generations per year. Unlike beetle larvae, larvae of aculeate Hymenoptera are not able to find their own food and instead rely on the provisions brought by their parent (pollen and nectar in bees, or preyed arthropods in wasps). They also do not move through their feeding substrate like saproxylic beetle larvae do (Potts et al., 2005; Michener, 2007; Westerfelt et al., 2015; Roberts, King and Milam, 2017). Bee and wasp larvae are restricted to brood cells their parents built. This means the nesting substrate – cavity or hole – does not need to be particularly large with larger ones simply accommodating more brood cells. Also, nest building bee or wasp females try, through various means, to optimize the size of the brood cells for the size of the provision as well as the growing larva, leaving as little unused space as possible (Budrys, Budriene and Nevronyte, 2010). This way maximal number of brood cells can be constructed in limited amount of nesting substrate (hollow branch, beetle gallery, crack in wood). The nesting cavity is usually also treated with antibacterial secretions by the parent to prevent possible contamination of the brood cells and their contents (Madden et al., 2013; Weiss, Parzefall and Herzner, 2014; Baracchi and Tragust, 2015). The nest is also well protected from most predators and parasites, as it is not only enclosed in a cavity but reinforced with other materials, like mud, resin or wood dust. On top of that, most cavity-nesters build a plug at the cavity entrance after all the brood cells are build (Michener, 2007). This limits the number of possible nest invaders to those who evolve specialized behaviour which allows them to locate and either enter the nests while it is being build, or enter a completed nest by destroying or bypassing the plug (Groulx and Forrest, 2018; Minckley and Danforth, 2019). Because of the treatment of the nesting cavities and little to no damage done to the substrate by the larvae and adults, the nesting sites can be used repeatedly without being depleted and hence, the nesting substrate amount probably limits woodland aculeate Hymenooptera less (Michener, 2007; Harmon-Threatt, 2020; Pinilla-Gallego, 2022). Concurrently, the amount of foraging resources or prey choice in the vicinity and broader area around nest sites, likely strongly affect the selection of nest place.

5.3. Flight ability

Dispersal ability of most insects is corelated with their maximal flight distances. These are, however, hard to find for many insects due to their small size and the usefulness of different measuring methods differing among taxa. Maximal flight distances in some saproxylic beetles are known but mostly for large flagship species or species of economic importance, like bark beetles (Jones et al., 2019; Doležal, Okrouhlík and Davídková, 2016). Such maximal flight distances can be as long as several kilometres. This, however, is usually true for only small percentage of individuals, with most populations being fairly sedentary (Feldhaar and Schauer, 2018). It is also worth noting that a long-distance dispersal for saproxylic beetles is often a one-time event, often prompted by a change in local habitat or natural vectors such as wind or fire (Hedin et al., 2008; Bae et al., 2020; Müller et al., 2020). While dispersal ability for aculeate Hymenoptera is high, it is usually the maximal foraging distances which limit their ecological behaviour. The foraging distances are known to correlate with body length and are in tens of metres for smaller species, in hundreds of metres for large species, and can be over a kilometre for large social species such as hornets or bumblebees (Greenleaf et al., 2007; Lihoreau, Chittka and Raine, 2010; Zurbuchen et al., 2010).

5.4. Sampling methods

Due to difference in flight abilities and ecology some sampling methods are considered less suitable for one or the other group. Large and characteristic species can be individually surveyed via exit holes and galleries (Albert, Platek and Cizek, 2012; Zan et al., 2017). Similarly, pheromone traps are selective sampling method usable only for narrow spectrum of species. To survey individual microhabitats or items, various emergence traps or sticky traps are also used

(Weslien and Lindelöw, 1989; Bashir, Alvi and Naz, 2014; Dearden et al., 2023). Typical sampling method for beetles are window or flight-interception traps and pan or Moericke traps are used for Hymenoptera (Abrahamczyk, Steudel and Kessler, 2010; Bouget, Larrieu and Brin, 2014; Gezon et al., 2015; Sebek et al., 2016). However, even using flight-interception traps it is possible obtain representative sample of the forest Hymenoptera foraging communities (actively flying individuals) (Rubene, Schroeder and Ranius, 2015). In this aspect the flight-interception traps are somewhat similar to Malaise traps, but unlike Malaise traps, they are commonly sturdier and can also be more effectively placed in higher positions or in areas of dense vegetation (Bouget, 2005; Kozel et al., 2021; Weiss et al., 2021). This still only addresses the foraging or active individuals. Flight-interception traps, however, make up for it by their ability to be exposed for entire season (Campbell and Hanula, 2007; Westerberg et al., 2021; Acharya et al., 2022) The nesting communities i.e. what species actually build nests on site, are far harder to study. Individual surveys of natural nesting cavities or built nests are unreliable and time-consuming, rarely yielding useful data. Here, use of various emergence traps like trap-nests is an invaluable trapping method for the study of nesting communities (Tscharntke, Gathmann and Steffan-Dewenter, 1998; Loyola and Martins, 2008; Bogusch, Bělastová and Heneberg, 2017). Their use is, however, often connected to research of distance-based differences in communities between assumed source and sink type habitats like forest – orchard, forest -brownfield or forest edge – forest interior (Taki et al., 2008; Loyola and Martins, 2011; da Rocha-Filho et al., 2017). Use of trap-nests in the study of habitat selection by aculeate Hymenoptera is less common, likely also due to cavity-nesters being only about 20% of the diversity of aculeate Hymenoptera (Bogusch and Horák, 2018).

6. Conservation in practice

Conservation efforts targetting saproxylic beetles and those targetting woodland aculeate Hymenoptera are usually disparate, carried out in forested environments or in open habitats, respectively.

In forested areas, conservation effort to protect woodland biodiversity often involve management replicating disturbances, canopy thinning, canopy diversification, selective and retention logging (Koch Widerberg et al., 2012; Heikkala, Martikainen and Kouki, 2016; Chase et al., 2023). This creates more open habitat patches which benefit the nectar and pollen dependent Hymenoptera (Bennett et al., 2014; Lettow et al., 2018; Eckerter et al., 2021; Rappa et al., 2024). Outside and inside of forest environments, retention of deadwood and forest legacies such as old and veteran trees is often suggested to help conserve the local woodland or deadwood dependent biodiversity (Zolotarjova, Kraut and Lõhmus, 2016; Doerfler et al., 2017, 2018; Burton, Jentsch and Walker, 2020). Here the benefits of deadwood retention for many organism groups is also highlighted in research and practice alike (Doerfler et al., 2020; Eckerter et al., 2021; Chase et al., 2023). Such actions seldom target bees and wasps specifically.

When conservation effort target bees and wasp, it often focuses on open habitats like steppes, meadows, orchards and pastures (Stefan-Dewenter and Leschke, 2002). Here, the creation of resource rich, open habitats is generally recommended as well as emulation of disturbances which prevent succession onset (Sjödin, Bengtsson and Ekborn, 2008; Hoehn, Stefan-Dewenter and Tscharntke, 2010; Whittet, Hope and Ellis, 2015; Viljur and Teder, 2016; Hilmers et al., 2018). Also, limiting the number of domesticated honeybee hives to lessen competition, is often suggested in protected areas even though the effectiveness of such measures remains uncertain (Stefan-Dewenter and Tscharntke, 1999). However, management for nesting opportunities is largely absent from practice (Potts et al., 2005; Grundel et al., 2010).

Therefore, management and conservation practices that focus on both saproxylic beetles and woodland associated aculeate Hymenoptera at the same time are rare. The chapters of the present thesis try to shed more light on congruences and discrepancies in drivers and patterns of biodiversity of these two groups.

7. Thesis chapters

In the present thesis, I focused on the woodland aculeate Hymenoptera, their selection of preferred habitat, reaction of their communities to management and the similarities or differences from patterns of saproxylic beetle communities. While woodland bee and wasp species richness and community composition trends roughly follow those of beetles, the underlying mechanism can be quite different and worth understanding. The chapters of this thesis are all published research articles expanding knowledge on the problematic of the diversity and species richness of aculeate Hymenoptera in woodland habitats with different structure and management / disturbance histories. The chapters are sorted chronologically based on the date in which the articles were published. Chapter I and II are co-authored by the author of the thesis. Chapter III and IV of the thesis are first-authored publications.

In chapter I - **Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity** the effect of disturbance and salvage logging on biodiversity of multiple taxonomic groups was studied together with the impact of disturbance and salvage logging on drinking water quality. The impacts of forest disturbance and salvage logging on forest associated biodiversity, with attention to saproxylic taxonomic groups, is discussed together with possible impacts on water quality.

Chapter II - **Estimating retention benchmarks for salvage logging to protect biodiversity** aims to estimate the minimal area of disturbed forests, which needs to be left without salvage logging to preserve the diversity of various forest associated organism groups. Here, a set of benchmarks is proposed, which allow informed conservation decisions about salvage logging in disturbed forests to be made.

Chapter III - **Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging** also describes the effect of disturbance and salvage logging on communities of forest insects (saproxylic beetles, cavity and non-cavity nesting bees and wasps), but with addition of retention logging, a practice where only most valuable timber is removed and the rest left on site for the natural processes. The possible main drivers of the community composition and diversity of studied insect groups are described, and conservation implications discussed.

Finally, chapter IV - **Microbiotope selection in saproxylic bees and wasps (Hymenoptera, Aculeata) – Cavity-nesting communities in forests and wooded pastures are affected by variation in openness but not deadwood** describes the nesting preferences of saproxylic cavity-nesting bees and wasps in wooded pasture and forest habitats in microbiotopes with different canopy openness. This study specifically targets deadwood-nesting bees and wasp by means of wooden trap-nests, which makes it unique among other studies focusing on nesting requirements.

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Chapter I

Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity

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Chapter I

Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity

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Abstract

Forests host most terrestrial biodiversity and provide important ecosystem services, including the provision of drinking water. Increasing frequency and intensity of natural disturbances and subsequent salvage logging may impact both biodiversity and drinking-water quality. However, empirical evidence and particularly that generated from long-term studies, is scarce. Using data obtained from the monitoring of streamwater between 1985–2018 and mid-term data on biodiversity of twelve species groups, we quantified the combined effects of natural disturbances and salvage logging. We used generalized additive models to test the effects of cumulative disturbed and salvage-logged areas on annual maximum nitrate and dissolved organic carbon (DOC) concentrations. We used generalized mixed-effects models to test the effect of management (disturbed unlogged, disturbed logged and undisturbed, intact forest) on species numbers of studied taxa. We found that forest disturbances led to a temporal increase of nitrate concentration in streamwater, yet remaining far below 50 mg L^{-1}, the limits recommended by the World Health Organization. Salvage logging did not exert any additional impact on nitrate and DOC concentrations, and hence did not affect streamwater quality. Natural disturbances increased the biodiversity in eight out of twelve species groups. Salvage logging additionally increased the biodiversity of five species groups related to open habitats, but decreased the biodiversity of three deadwood-dependent species groups. We conclude that neither natural forest disturbances in watersheds nor associated salvage logging have a harmful effect on the quality of the streamwater, which is used for drinking water. Setting aside naturally disturbed areas would promote the conservation of deadwood-dependent species.

Keywords

Post-disturbance management, windthrow, ecosystem services, forested watershed, nitrate, dissolved organic carbon

1. Introduction

The world's forests store vast amounts of carbon, provide important ecosystem services to humans and host a considerable part of the planet's terrestrial biodiversity (FAO and UNEP, 2020). In recent decades, natural disturbances, such as wildfire, windstorms and insect outbreaks, have severely disrupted large areas of the world's forests at an unprecedented rate (Seidl et al., 2014). Natural disturbances can cause a decreased interception, increased surface runoff, soil moisture, erosion and leaching of soil nutrients into streams (Mikkelson et al., 2013; Moore and Richardson, 2012). In terms of biodiversity, however, species richness, habitat quality and other diversity indices mostly increase in disturbance-affected forests (Beudert et al., 2015; Thom and Seidl, 2016).

In Europe, windstorms are the most important disturbance agents, responsible for 53% of the total damage in forests between 1950 and 2000 (Schelhaas et al., 2003). Forest stands affected by windstorms often enable the rapid growth of bark beetle populations (Seidl et al., 2014), which accounted for 8% of the total damage in European forests between 1950 and 2000 (Schelhaas et al., 2003). Although the interactions between windthrow and bark beetle outbreaks are well understood (Kulakowski et al., 2017), those between windthrow and post-disturbance logging have been rarely investigated, especially through the use of long time series (Leverkus et al., 2018).

Despite its detrimental effects on biodiversity (Thorn et al., 2018), salvage logging is the most common post-disturbance management practice (Müller et al., 2019). As the extent, frequency and intensity of natural disturbances increases worldwide due to climate change (Seidl et al., 2017), the area of salvage logging in both managed and protected forests has increased as well (Leverkus et al., 2018; Müller et al., 2019). The main justifications for salvage logging are the recovery of economic value from disturbance-affected timber as well as recovering the provision of ecosystem services (Müller et al., 2019). The effects of salvage logging on biodiversity have been examined, but the majority of studies compared salvage-logged with unlogged (no intervention) plots rather than using intact forest stands as the control treatment (Fontaine et al., 2009; Zmihorski, 2010). In addition, while the response of biodiversity to salvage logging during the first 5 years after the disturbance has been investigated (Thorn et al., 2018), studies of longer time series are scarce (Thorn et al., 2020).

Natural disturbances and subsequent salvage logging promote the mineralization of organic matter and nitrification in soils under humid and seasonal warm climate conditions (Vitousek et al., 1979), leading to higher availabilities of dissolved nitrogen (as NH_4^+ and NO_3^-) and dissolved organic carbon (DOC) in soils. The reduction of canopy cover that follows a natural disturbance not only drastically reduces nutrient uptake by plants, it also decreases evapotranspiration losses, leading to higher soil water flows (Andréassian, 2004) and increased leaching of nitrates and DOC into streams (Laudon et al., 2009; Strohmeier et al., 2013). When nitrate concentrations in drinking water exceed 50 mg L^{-1}, water becomes a major source of total nitrate intake for human consumers, which in bottle-fed infants may result in fatal disorders (World Health Organization, 2016). DOC is also an important water quality parameter, it has the potential to reduce soil water pH, transport metals and organic contaminants as well as nutrients into streams (Ågren et al., 2010; Kaplan and Newbold, 2000), and may induce the formation of cancerogenic disinfection by-products in drinking water (Mikkelson et al., 2013). In fact, increasing DOC concentrations in many streams and lakes in the boreal forests in Europe and North America have recently been measured (Garmo et al., 2014; Monteith et al., 2007).

The amount and type of soil disturbance can cause changes in water regimes and water quality in mountainous watersheds. For instance, severe wildfires reduce natural soil water repellency by scorching the surface soil layer (Martins et al., 2020). Furthermore, post-fire salvage logging additionally compacts burned soils (Malvar et al., 2017), resulting in a greater water discharge, increased erosion, turbidity, export of solutes and nutrients to streamwater (Silins et al., 2014; Smith et al., 2012). However, the impact of salvage logging on water quality after windthrow and bark-beetles are poorly understood as majority of the studies concern post-fire salvage logging (Leverkus et al., 2020). In addition there is a lack of mid- to long-term studies about salvage logging effects on water quality (Leverkus et al., 2020).

In general, biodiversity response to forest disturbances and salvage logging is largely determined by changes in insolation and deadwood amounts (Thorn et al., 2018). Compared to intact forests, windthrow increases deadwood amount and insolation, whereas salvage logging reduces deadwood amount and may increase additionally insolation and surface temperatures (Fontaine et al., 2010). As result, the species richness of deadwood-dependent (i.e. saproxylic) taxa, such as saproxylic beetles, wood-inhabiting fungi, epixylic lichens and bryophytes, can increase following disturbances (Beudert et al., 2015), but may decrease following salvage logging (Thorn et al., 2018). On the other side, species groups that do not rely on deadwood but benefit from increased insolation, such as vascular plants, epigeic spiders, lichens and bryophytes, have higher species richness in disturbed forests and salvage-logged forest as well (Thorn et al., 2018).

We analyzed data from long-term streamwater monitoring conducted in five watersheds and associated mid-term biodiversity data of 12 species groups with largely differing relation to deadwood and insolation. Our aim was to examine the effects of natural disturbances and salvage logging on: i) maximum concentrations of nitrate and dissolved organic carbon (DOC) in the runoff that provides drinking water and ii) species diversity within 12 species groups.

We expected that nitrate and DOC concentrations would increase within several years after the natural disturbances. A reduction in nitrate and DOC concentrations in salvage-logged watersheds would mean that deadwood extraction would effectively reduce leaching, affecting water quality positively. An increase in nitrates and DOC in salvage-logged watersheds would mean that possibly due to soil disturbance salvage logging operations would affect water quality negatively. In terms of biodiversity effects, we expected that natural disturbance would increase species numbers of deadwood-dependent groups and groups related to open habitats. Salvage logging would decrease species numbers in deadwood-dependent groups but would additionally facilitate open-land groups.

2. Materials and Methods

2.1 Study area

The study was conducted in the Bavarian Forest National Park (Fig. 1), south-eastern Germany (49°070 N, 13°310 E). The park is dominated by subalpine forests of Norway spruce (*Picea abies* (L.) H. Karst). Annual precipitation ranges from 1300 to 1800 mm and the annual mean air temperature is 3.0–4.0°C in the valleys and summit areas and 8°C in medium slopes areas (Bässler et al., 2010, updated in 2019).

In January 2007, the windstorm referred to as 'Kyrill' struck Central Europe. The storm hit the entire park, including the studied catchment areas, with intensities ranging from single tree felling to the downing of complete stands (Thorn et al., 2017). From the 1000 ha of mature Norway spruce forests felled by the winds, park managers left four larger patches, totaling ~200 ha, unlogged to establish study plots for biodiversity surveys. On the remaining 800 ha, storm-felled trees were removed by post-disturbance logging, which continued until August 2007. During logging operations, branches were cut off the trunk and left on the ground, and the main trunk was removed. Logging reduced the deadwood amount in all logged areas from ~300 m^3/ha to ~50 m^3/ha (Thorn et al., 2015, 2014).

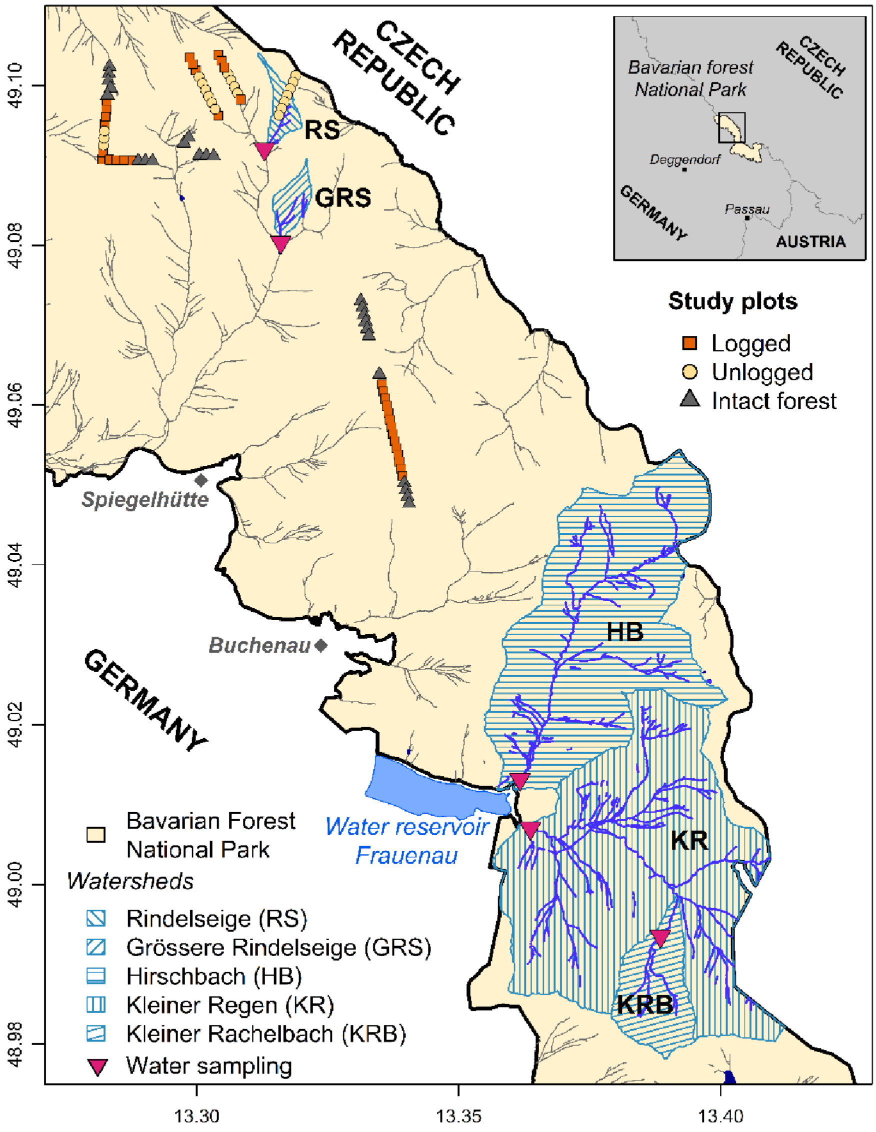

Figure 1. Watersheds and sampling plots in the Bavarian Forest National Park. The contour lines represent the elevation above sea level, and the blue lines the streams of the studied watersheds.

2.2 Forest cover monitoring

The amount of disturbed and salvage-logged area within the watersheds was estimated by identifying bark beetle infested and wind-thrown spruce trees on annually recorded color-infrared images (Lausch et al., 2011). Afterwards, the percentage of disturbed and salvage-logged area for every single watershed was plotted as accumulated totally disturbed area over time (Fig. 2, Fig. 3).

2.3 Water monitoring

Data for water chemistry were collected during a long-term monitoring program of the Bavarian Forest National Park. The chemical composition of the streamwater was determined within five watersheds: Rindelseige, Grössere Rindelseige, Hirschbach, Kleiner Regen and Kleiner Rachelbach (Fig. 1, Table 1), all of which were dominated by Norway spruce. The water monitoring for the watersheds Hirschbach and Kleiner Regen started in 1985, for Kleiner Rachelbach in 1987, and for Rindelseige and Grössere Rindelseige in 2000. Forests in all watersheds were not affected by stand-replacing natural disturbances before the beginning of the water monitoring. Forests in the national park are important for water provision in the region, for instance, the Frauenau drinking water reservoir (Fig. 1) is almost entirely fed by the Hirschbach and Kleiner Regen watersheds. Mean modeled annual precipitation (mm) and runoff (mm) from 1981 to 2015 for the five watersheds was as follows: Ringelseige (1875 mm / 1340 mm), Grössere Rindelseige (1552 mm / 991 mm), Hirschbach (1635 mm / 1079 mm), Kleiner Regen (1637 mm / 1106 mm), Kleiner Rachelbach (1741 mm / 1292 mm) (Klöcking, 2019). Water samples were taken manually in 1- or 2-week intervals at or near the catchment outlets (for exact locations see Fig. 1). Sampling as well as sample storage and preparation strictly followed international instructions (ICP-Forests, 2010; ICP-Integrated-Monitoring, 2010). Chemical components were analyzed by certified laboratories of state institutes using ion chromatography for nitrates (DIN EN ISO 10304-1, 1992) and elemental analysis after UV oxidation for dissolved organic carbon (DIN EN 1484-H3:1997-8, 1997). The hydrochemical data of Hirschbach, Kleiner Regen and Kleiner Rachelbach were provided from the Bavarian Environment Agency (LFU) those of Rindelseige and Grössere Rindelseige by the Bavarian Forest National Park.

2.4 Biodiversity sampling

Biodiversity sampling was part of a long-term monitoring program of the Bavarian Forest National Park that was initiated after the windstorm “Kyrill” in 2007. The main aim of the monitoring program was to collect representative biodiversity data in disturbed unlogged areas and disturbed salvage-logged areas. In 2018, the monitoring program was extended by adding plots in intact forests. The study plots were placed in the northern part of the national park and covered representatively logged, unlogged and intact forests in the study area (Fig. 1). The number of plots differed slightly among the studied taxa (for details, see Table S1). Twelve species groups were sampled in the study: epigeic spiders, ants, bees and wasps, saproxylic beetles (i.e. beetles dependent on or associated with living as well as dead trees; Alexander 2008), non-saproxylic beetles, wood-inhabiting fungi, epigeic bryophytes, epigeic lichens, epixylic bryophytes, epixylic lichens, vascular plants and birds. Bees and wasps, saproxylic beetles and non-saproxylic beetles were trapped using flight-interception traps placed at the center of every study plots (Thorn et al., 2014). Epigeic spiders and ants were trapped using two pitfall traps per plot. The two pitfall traps were placed within a 10 m buffer around the center of each plot, at least 10 m apart from each other. Bryophytes and lichens were mapped on deadwood objects (i.e. epixylic) and on the ground (i.e. epigeic) separately. Wood-inhabiting fungi, epixylic bryophytes and epixylic lichens were sampled on five deadwood objects that were randomly selected in a 20 m radius around the center of each plot (Thorn et al., 2016a). The deadwood objects we selected in 2007 for logged and unlogged plots, and in 2018 for intact forest plots. Over the years, some objects on logged and unlogged plots decomposed, hence their sampling number varied over years for these two treatments. In 2018, a total of 138 deadwood objects on logged and unlogged and 100 object on forest plots were surveyed. Vascular plants, epigeic mosses and lichens were sampled on circular plots (relevees) of 200 m^2 around each plot's center. Birds were surveyed five times during the breeding season by applying fixed-radius (50 m radius) point-counts with 5-min count intervals per plot (Thorn et al., 2016b). All bird counts were conducted during the morning hours in good weather conditions. The biodiversity data were aggregated to the plot level for each year for subsequent analyses. Due to financial and personnel constraints, not all treatment types were sampled in all years, except birds. However, 11 years after the disturbance all 12 species groups in all habitat types were examined in a comprehensive assessment.

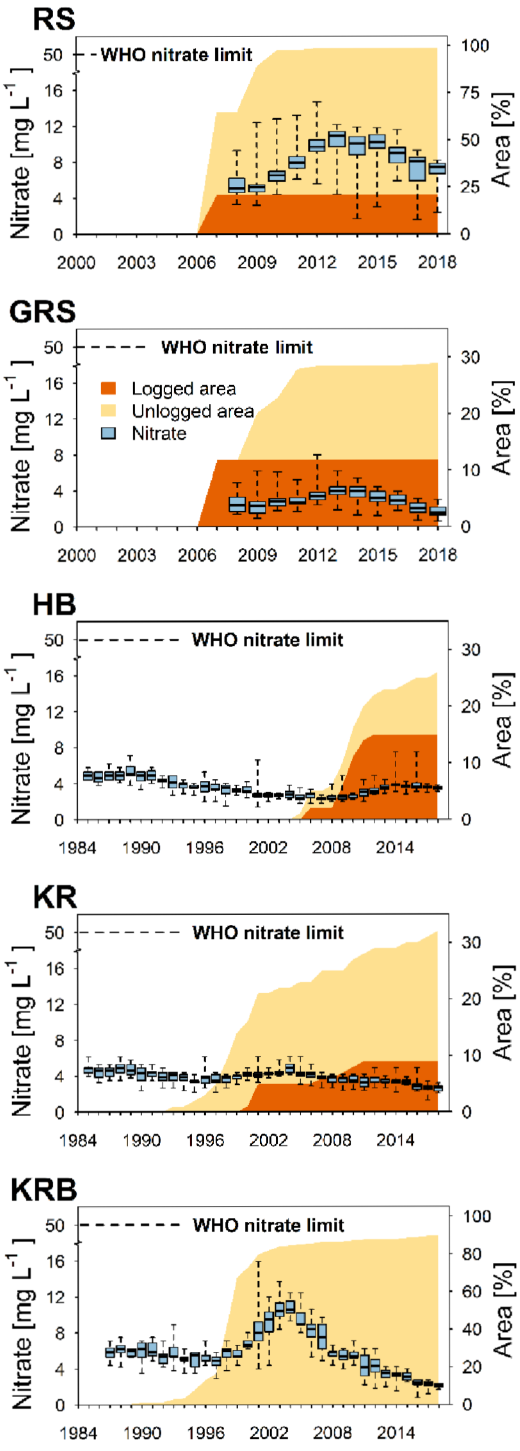

Figure 2. Concentrations of nitrate in the streamwater of five watersheds in the Bavarian Forest National Park: RS: Rindelseige, GRS: Grössere Rindelseige, HB: Hirschbach, KR: Kleiner Regen, KRB: Kleiner Rachelbach. Note the differences in the y-axis.

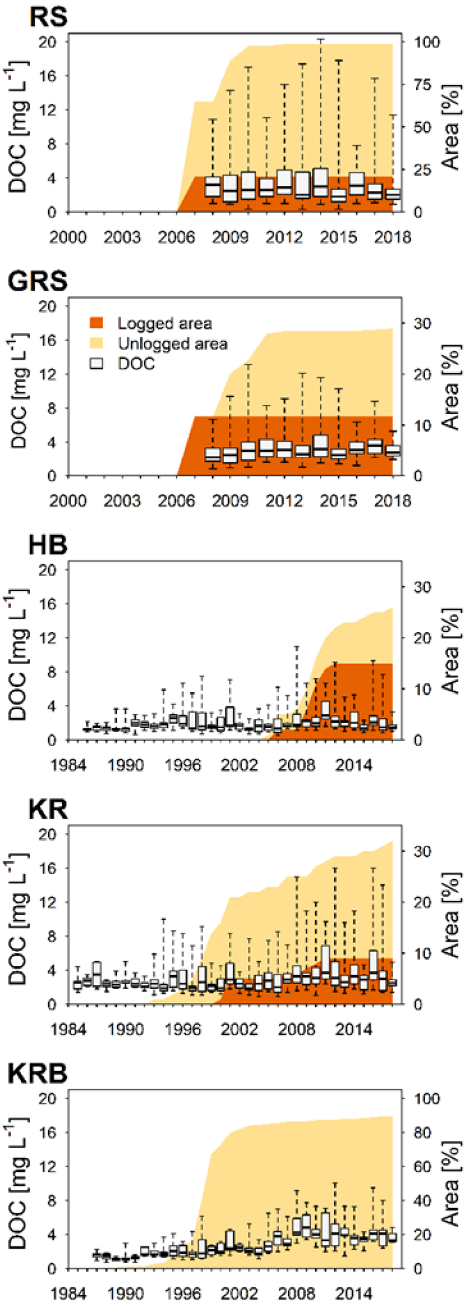

Figure 3. Concentrations of dissolved organic carbon (DOC) in the streamwater of five watersheds in the Bavarian Forest National Park: RS: Rindelseige, GRS: Grössere Rindelseige, HB: Hirschbach, KR: Kleiner Regen, KRB: Kleiner Rachelbach. Note the differences in the y-axis.

2.5 Data analysis

The analyses were carried out in R 4.0.1 (R Development Core Team, 2020). Generalized additive models (GAM) were applied to test the effects of annual and cumulative disturbed and salvage-logged areas on annual maximum nitrate and DOC concentrations for the five watersheds (Wood, 2006). The explanatory variables were the percentages of disturbed and salvage-logged area, as the linear terms, and the proportional annual increase in disturbed area (%), as well as, when applicable, the proportional annual increase in salvage-logged area (%) as smooth terms. Because the peaks in maximum nitrate and DOC concentrations were time-delayed, an additional explanatory time-lagged variable was included. For the percentages of disturbed and salvage-logged areas, 10 time lags were created, i.e. each of the original values was lagged between 1 and 10 years. The best fitting time lag was determined by re-running the model, replacing every one of the ten time-lagged variables while keeping the remaining variables constant. The final model was selected based on the highest adjusted r^2, with the corresponding time-lagged variables (Table S2). Time-lagged variables were not used for watersheds Rindelseige (RS) and Grössere Rindelseige (GRS) as the models were unstable. Following an analysis of the temporal correlation structure of the model residuals, using the autocorrelation function (*acf*) and the partial autocorrelation function (*pacf*; package '*stats*'), we included a first-order autocorrelation as the correlation structure in the GAMs (Fig. S2).

Changes in the number of species were modeled using linear mixed-effects models with a Poisson error distribution (function *glmer* from *lme4* package; Bates et al., 2015). Separate models were fitted for all species groups (Table S3), with the number of species as the response variable and the treatment (disturbed, logged, forest) as the explanatory variable. For each group with more than one study year, the effects of disturbances and salvage logging were tested separately for each year by including an interaction term between study year and treatment as an additional explanatory variable. To account for possible spatial autocorrelations, a spatial autocovariate term of the geographical coordinates of the plots was included as a fixed effect in all models (function *autocov_dist*; package *spdep*; Bivand et al., 2013). Differences across the study plots and repetitive sampling within these plots were accounted for using plot identity as a random effect. This was followed by pairwise-comparisons based on general linear hypothesis tests with simultaneous adjustment of the p-values (function *glht*, package *multcomp*; Hothorn et al., 2008), to test for differences between single treatments during every studied year. The general linear hypothesis tests are used to control the overall type I error rate when multiple null hypothesizes are tested simultaneously (Hothorn et al., 2008). Only significant differences ($p < 0.05$) are shown, indicated as superscript letters above the boxplots (Fig. 3).

A possible mass effect influencing the number of saproxylic beetles was taken into account by standardizing the number of sampled plots—as a proxy for deadwood resources—by extrapolating the species number to 40 plots within all treatments, using rarefaction and extrapolation curves (*iNEXT* package; Hsieh et al., 2016).

3. Results

3.1 Effects on water quality

The studied watersheds (Fig. 1) were affected to different degrees by natural disturbances, with the overall largest proportion of cumulative forest dieback in the Rindelseige watershed (98.7%), followed by the Kleiner Rachelbach (89.5%), Grössere Rindelseige (28.9%), Hirschbach (26%) and Kleiner Regen (25%) watersheds.

Annual maximum nitrate concentrations increased steadily following a disturbance, with a time-delayed peak (Fig. 2). The modeling results showed that the maximum nitrate concentration increased markedly in the most severely affected watersheds but the increase was significantly related only to the percent increase of annually disturbed area in the Kleiner Rachelbach watershed and to the 6-year-lagged percent of disturbed area for the Kleiner Regen and Kleiner Rachelbach watersheds (Table S2). Nonetheless, in none of the watersheds did the maximum nitrate concentration exceed 16 mg L^{-1}, a value far below the World Health Organization limit of 50 mg L^{-1}. According to this result, general water quality did not suffer from a natural disturbance (windthrow and bark beetles) or salvage logging. The percent of salvage-logged area was not significantly associated with the maximum nitrate concentration for any of the studied watersheds (Table S2).

Unlike nitrates, there were no distinct peaks in the maximum DOC concentration, irrespective of the forested area affected by natural disturbance and subsequent salvage logging (Fig. 3). The modeling results showed that the annual maximum DOC concentrations were significantly associated only with the increase in the annual disturbed area for the Hirschbach watershed as well as the percent disturbed area and the 1-year-lagged percent disturbed area of the Kleiner Rachelbach watershed (Table S2). There was no significant association between the salvage-logged area and the maximum concentrations of DOC in streamwater.

3.2 Effects on biodiversity

The 12 species groups sampled in this study represented 1341 species. Non-saproxylic beetles (n = 332) were the most species-rich group followed by saproxylic beetles (n = 259), wood-inhabiting fungi (n = 155), and epigeic spiders (n = 138) (Fig. 4). Epigeic lichens (n = 15), and ants (n = 13) had the fewest number of species.

Forest dieback caused by natural disturbances significantly affected most species groups, such that the species numbers of plants, bees and wasps, ants, epigeic spiders and non-saproxylic beetles were higher on unlogged than on forested plots (Fig. 4I–L, Table S3). However, the removal of deadwood resources during salvage logging significantly altered the effects of a preceding natural disturbance, as with few exceptions consistently higher numbers of species from saproxylic groups, i.e. epixylic lichens, wood-inhabiting fungi and saproxylic beetles, were detected on unlogged than on salvage-logged plots (Fig. 4). Conversely, the number of species in the non-saproxylic groups, i.e. epigeic bryophytes, epigeic lichens, ants, spiders and non-saproxylic beetles, was higher on logged plots (Fig. 4). Nonetheless, these differences for the non-saproxylic groups were only significant 11 years after the disturbance. Bird species numbers varied the most between treatments and years, with undisturbed forested plots consistently hosting the largest number of species throughout the 11-year study period (Fig. 4H).

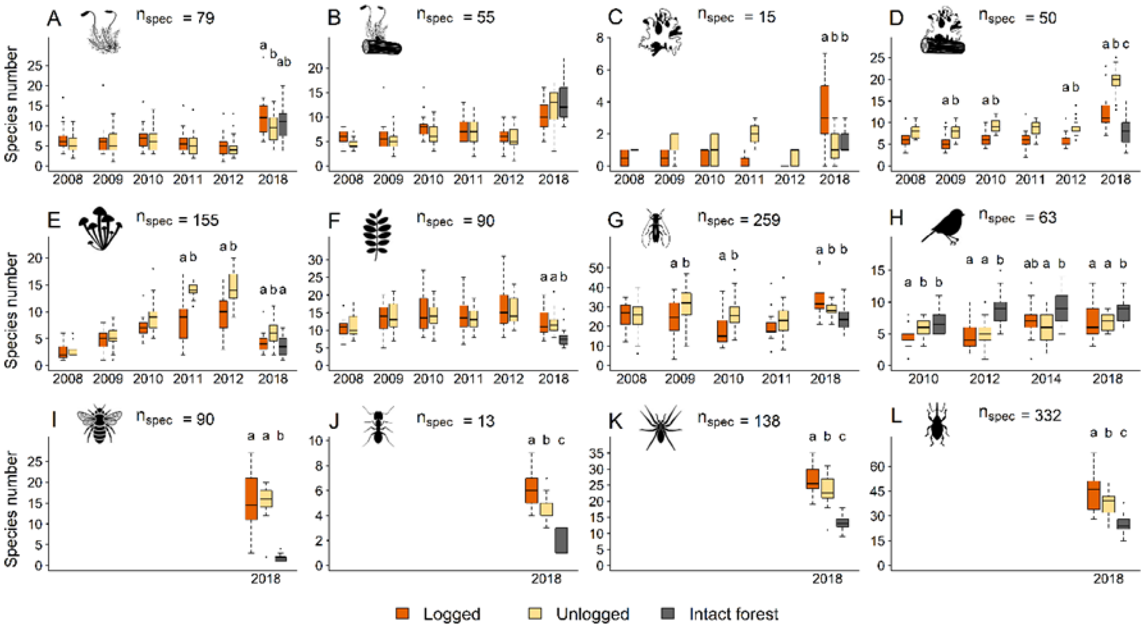

Figure 4. Species numbers of 12 taxa sampled in salvage-logged disturbed forest (logged), unlogged disturbed forest (unlogged) and undisturbed mature spruce forest (intact forest) plots in the Bavarian Forest National Park. A) Epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) fungi, F) plants, G) saproxylic beetles, H) birds, I) bees and wasps, J) ants, K) epigeic spiders and L) non-saproxylic beetles. n_{spec} indicates the total number of sampled species. Superscripts above the boxplots denote significant differences ($p < 0.05$) in species numbers between the treatments within single years.

4. Discussion

Using long-term water monitoring data, we demonstrated that an increase in naturally disturbed areas was followed by a temporal increase in the annual maximum concentrations of nitrates (Fig. 2) and, to a lesser extent, of DOC in streamwater (Fig. 3). Salvage logging did not significantly change the maximum concentrations of nitrates or DOC (Table S2) but it did lead to contrasting responses of biodiversity. We registered an increase of species numbers in non-saproxylic, open-land species groups but also a considerable decline in species numbers of saproxylic species groups (Fig. 4).

The maximum nitrate concentrations did not exceed the WHO drinking water limit of 50 mg L^{-1} in any of the studied watersheds. These results support the findings from studies in bark-beetle-killed (Beudert et al., 2015), burned (Smith et al., 2012) and wind-felled (Hartmann et al., 2016) forests, in which maximum nitrate concentrations did not exceed the WHO health limit. Thus, the main natural-disturbance agents across the Northern Hemisphere seem to have few overall effects on water quality (Leverkus et al., 2020).

The peak in maximum nitrate concentrations 3–5 years after the disturbance event (Fig. 2) is in agreement with the findings of Hartmann et al. (2016), who registered peaks of dissolved inorganic nitrogen (mainly nitrate) ~4 years after a windthrow. In our study, in the Kleiner Regen and Kleiner Rachelbach watersheds the peak in nitrates was best explained by the 6-year lag in the percent disturbed area (Table S2), which is an independent lagged variable. While not reaching significant levels, the maximum nitrate concentrations for the Rindelseige watershed also had a time lag of 6 years (Fig. 2). These results indicate that the maximum concentration of nitrates in those watersheds depended on the percent of annually disturbed area 6 years earlier. A return to the pre-disturbance level of nitrates occurred ~10 years after the disturbance event (Fig. 2), which is similar to the findings from other watersheds in the Bavarian Forest National Park (Beudert et al., 2015; Huber, 2005). A number of processes are responsible for the time-delayed increase of nitrates after the disturbance and the return to pre-disturbance nitrate levels. During the first years after a disturbance the sparse understory vegetation is unable to take up and assimilate the surplus of nitrogen in the soil, resulting in the lateral transport of nitrates through near-surface soil layers into streams as well as vertical transport towards aquifers. This is the reason for the time-delayed increase of nitrates. The nitrate concentrations return to their pre-disturbance level when regeneration of the disturbed stand progresses, the nitrogen cycle is again controlled by vegetation uptake, which reduces the leaching losses of nitrates such that their concentrations in groundwater and streams fall to and below pre-disturbance levels (Likens et al., 1978).

Compared to undisturbed forests, an increase of DOC concentrations in surface water has been reported after clear-cut logging in European boreal forests (Laudon et al., 2009) as well as after wildfire and consecutive salvage logging in Canadian boreal forests (Emelko et al., 2011). By contrast, we found no evidence of a significant relationship between the annual salvage-logged area and the maximum annual DOC concentration in streamwater (Table S2), indicating that salvage logging did not affect DOC. These diverging results can be explained by the generally deeper (≥ 1 m) soils in our study region than in boreal regions. Deeper soils allow the more effective sorption and stabilization of DOC in mineral soil (Kalbitz et al., 2000; Kalks et al., 2020) such that less DOC leaches into aquifers and streams.

However, maximum DOC concentrations increased significantly with the annual increase of disturbed area in the Hirschbach watershed as well as in response to increases in the percent disturbed area and the 1-year lag in disturbed area in the Kleiner Rachelbach watershed (Table S2). While the results for these two watersheds were significant, they deviated only slightly from the general DOC trend, which was similar in all studied watersheds irrespective of the percentage of disturbed area in each one (Fig. 3). Thus, the cumulative area of naturally disturbed forest seems to have little effect on the maximum DOC concentration.

DOC is composed of thousands of compounds, some of which can form harmful disinfection-by-products during chlorination, such as during water treatment (Mikkelson et al., 2013). Although there are no thresholds for DOC concentrations, water treatment generally becomes more expensive when the concentration surpass 4 mg L^{-1} (Emelko et al., 2011). In the watersheds in our study, DOC concentrations in streamwater were lower (2.39 mg L^{-1} on average) than in the streams of the Grosse Ohe catchment, located south of our study area, especially when the percentage of wet soils in their catchments was high (Beudert et al., 2012).

The inclusion of intact forest stands in our study revealed significant differences in species numbers between forested plots and logged as well as unlogged plots for most studied taxa (Fig. 4, Table S3). With the exception of birds, which had higher species numbers in forest areas, the species numbers for all taxa were significantly lower on forested plots (Fig. 4). These results highlight the importance of early successional forests as species-rich habitats (Swanson et al., 2011).

During most of the studied years, the species numbers of wood-inhabiting fungi, epixylic lichens and saproxylic beetles were significantly higher on unlogged than on logged plots (Fig. 4). For these deadwood-dependent species groups, the amount of deadwood is a major driver of species richness (Bässler et al., 2016). However, 11 years after the disturbance the number of species of saproxylic beetles was higher on logged than on unlogged plots, in contrast to the early years after the disturbance (Fig. 4G). In coniferous tree species, the abundance of saproxylic beetles typically decreases with increasing wood decay (Saint-Germain et al., 2007), as the reduced amount of nutrients in the later decay stages of deadwood attracts fewer saproxylic species over time (Kopf and Funke, 1998). In our study, the dieback after a windthrow caused a pulsed release of deadwood, resulting in a mass effect of coarse woody debris that most likely accounted for the higher species numbers on the unlogged plots. Support for this sequence of events is the fact that the differences between the three treatments became smaller when the species number was standardized by the number of investigated plots for the eleventh year after the disturbance (Fig. S1).

Species numbers of non-saproxylic groups (non-saproxylic beetles, bees and wasps, ants, epigeic spiders, plants, epigeic bryophytes and lichens) were significantly higher on logged plots 11 years after the disturbance (Fig. 4), most likely due to the increase in resource availability. Windthrow and associated bark-beetle infestations increase both the availability of light and the amount of deadwood (Wohlgemuth et al., 2019), while salvage logging typically reduces the amount of deadwood (Lindenmayer et al., 2008). Thus, on logged plots epigeic groups such as ants benefit from the higher insolation that increases the surface temperature, thereby facilitating species richness (Grevé et al., 2018; Kumischick et al., 2009). Similarly, the presence of epigeic bryophytes in the Bavarian Forest National Park is associated with open habitats, mainly due to their higher ground-surface temperatures (Raabe et al., 2010).

5. Conclusions

Our study showed that leaching of nitrates and DOC from disturbed watersheds does not pose a health risk to humans and conducting salvage logging does not change nitrate and DOC leaching into drinking water. However, the study also showed that natural disturbances in watersheds increase biodiversity of eight out of twelve species groups, mainly deadwood-dependent and species groups related to open habitats. Salvage logging additionally increased the biodiversity of five species groups related to open habitats, but decreased the biodiversity of three deadwood-dependent species groups. We conclude that neither natural forest disturbances in watersheds nor associated salvage logging have a harmful effect on the quality of the streamwater, which is used for drinking water. Setting aside naturally disturbed areas would promote the conservation of deadwood-dependent species.

Acknowledgments

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Appendix A. Supplementary materials

Species accumulation curves (Fig. S1), autocorrelation and partial autocorrelation functions (Fig. S2), studied species groups (Table S1), statistical summary for the effects of disturbed, and logged area on annual maximum concentrations of nitrate and dissolved organic carbon (Table S2), statistical summary for the effects of treatment on species numbers (Table S3) are available online.

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Appendix A. Supplementary materials

Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity

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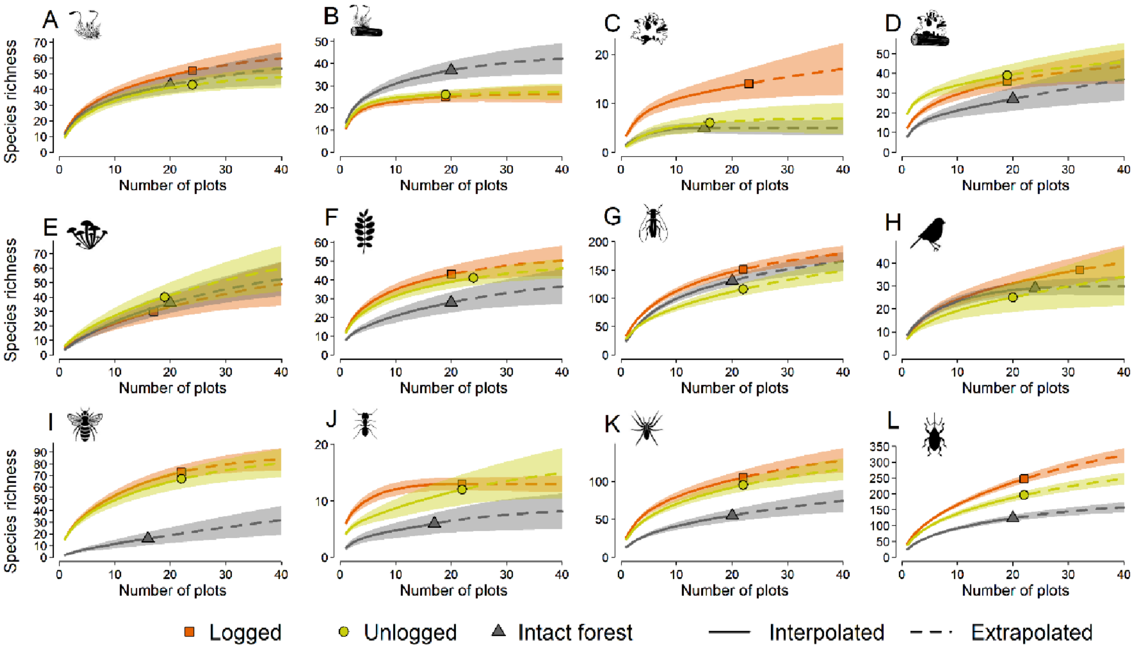

Figure S1. Estimated number of species for year 2018 in undisturbed mature spruce forests (intact forest), salvage-logged disturbed forest (logged) and unlogged disturbed forest (unlogged) plots. The estimation was performed with species accumulation curves (iNEXT R-package) by extrapolating the number of species to 40 studied plots.

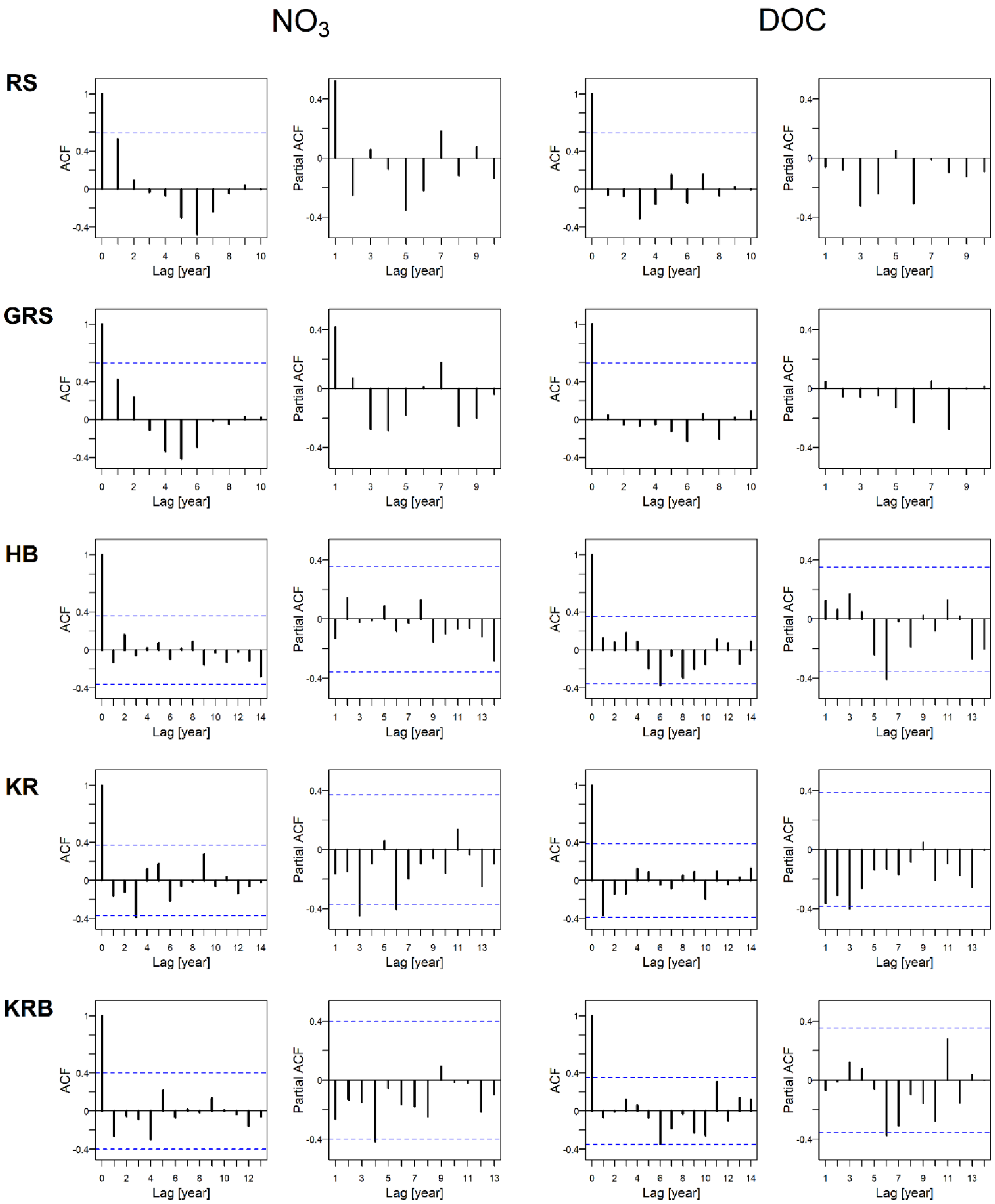

Figure S2. Estimates of the autocorrelation function (ACF) and partial autocorrelation function (partial ACF), for maximum concentrations of nitrate (NO_3) and dissolved organic carbon (DOC). The blue lines depict the threshold beyond which the autocorrelation is significant. The abbreviation depict the names of the water catchments (for details Fig. 1).

Table S1. Number of plots and survey details for twelve study species groups used to study the effects of natural disturbance and salvage logging on biodiversity, eleven years following a major windthrow.

Taxonomic group	**Plots**			**No. traps/deadwood objects**	**Sampling interval**	**Sampling frequency**	**Method**	**Reference**
	Logged	**Unlogged**	**Intact forest**					
Bees and wasps	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Saproxylic beetles	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Non-saproxylic beetles	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Epigeic Spiders	22	22	20	128	May–Sept	Monthly trap emptying	Pitfall traps	(Abraham, 2013)
Ants	22	22	20	128	May–Sept	Monthly trap emptying	Pitfall traps	(Abraham, 2013)
Wood-inhabiting fungi	17	19	20	238 (4-5 deadwood per plot)	July–Sept	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)
Epigeic bryophytes	24	24	20	na	Sept–Oct	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epigeic lichens	23	16	20	na	Sept–Oct	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epixylic bryophytes	19	19	20	238 (4-5 deadwood per plot)	Sept–Oct	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)
Epixylic lichens	19	19	20	238 (4-5 deadwood per plot)	Sept–Oct	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)
Vascular plants	24	20	20	na	July–Sept	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Birds	32	24	20	na	March-June	5 counts per season	Point-count sampling	(Bibby et al., 2000)

Table S2. Results of generalized additive models with first order autocorrelation testing the effect of disturbed and salvaged-logged area on annual maximum concentrations of nitrates and dissolved organic carbon in streamwater in five water catchments in the Bavarian Forest National Park. Increase of annual disturbed area (%) represents the annual increase in the proportion of naturally disturbed area. Increase of annual logged area (%) represents the annual increase of salvage-logged area as a fraction of the yearly disturbed area. X-years lag of disturbed/logged area (%) represent the number of years with which the values of the respective variable were lagged.

Catchments	Predictors	Annual maximum nitrate concentration				Annual maximum concentration of dissolved organic carbon (DOC)			
		Estimate	CI	t-Value	p-Value	Estimate	CI	t-Value	p-Value
Rindelseige (RS)	Intercept	4.76	-7.81 – 17.33	0.874	0.408	2.9	-22.76 – 28.56	0.261	0.801
	Disturbed area (%)	7	-6.80 – 20.80	1.169	0.276	12.06	-16.11 – 40.23	0.987	0.352
	Logged area (%)	0.99	-1.62 – 3.60	0.874	0.408	0.6	-4.73 – 5.93	0.261	0.801
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	1	1	0.782	0.402	1	1	0.115	0.743
Grössere Rindelseige (GRS)	Intercept	5.59	-0.08 – 11.26	2.272	0.053	7.28	-2.44 – 16.99	1.728	0.122
	Disturbed area (%)	-2.1	-24.09 – 19.88	-0.221	0.831	7.06	-30.59 – 44.71	0.432	0.677
	Logged area (%)	0.66	-0.01 – 1.32	2.272	0.053	0.85	-0.29 – 1.99	1.728	0.122
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	1	1	0.668	0.437	1	1	0.146	0.712
Hirschbach (HB)	Intercept	**5.81**	**3.36 – 8.25**	**4.96**	**<0.001**	**-5.24**	**-10.25 – -0.24**	**-2.19**	**0.041**
	Disturbed area (%)	-52.22	-134.06 – 29.61	-1.33	0.2	62.6	-181.17 – 306.37	0.54	0.6
	Logged area (%)	58.21	-60.87 – 177.29	1.02	0.32	153.2	-230.44 – 536.84	0.83	0.41
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	4	4	0.23	0.91	**4.75**	**4.94**	**2.71**	**0.049**
	Increase of annual logged area (%)	1	1	0.13	0.72	1	1	0.07	0.8

Catchments	Predictors	Annual maximum nitrate concentration				Annual maximum concentration of dissolved organic carbon (DOC)			
		Estimate	CI	t-Value	p-Value	Estimate	CI	t-Value	p-Value
	3-years lag of disturbed area (%)	1	1	0.31	0.59	1	1	0.04	0.85
	4-years lag of logged area (%)	1.08	1.16	0.03	0.92				
	2-years lag of logged area (%)					1.88	1.98	3.6	0.057
Kleiner Regen (KR)	Intercept	**4.73**	**3.20 – 6.26**	**6.53**	**<0.001**	**11.9**	**5.90 – 17.91**	**4.2**	**0.001**
	Disturbed area (%)	-2.35	-13.22 – 8.53	-0.46	0.65	-19.72	-82.54 – 43.10	-0.67	0.51
	Logged area (%)	9.43	-27.97 – 46.83	0.53	0.6	17.96	-239.11 – 275.03	1.49	0.88
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	4.42	4.66	0.6	0.72	1	1	0.01	0.98
	Increase of annual logged area (%)	1	1	1.17	0.68	2.99	3	0.66	0.58
	6-years lag of disturbed area (%)	**2.21**	**2.53**	**7.95**	**0.004**				
	8-years lag of disturbed area (%)					2.03	2.52	2.86	0.2
	2-years lag of logged area (%)	1	1	1.81	0.2				
	8-years lag of logged area (%)					1	1	0.02	0.89
Kleiner Rachelbach (KRB)	Intercept	**6.54**	**3.62 – 9.46**	**5.06**	**<0.001**	**2.88**	**1.84 – 3.92**	**5.68**	**<0.001**
	Disturbed area (%)	1.27	-2.66 – 5.20	0.73	0.48	**3.93**	**2.26 – 5.60**	**4.83**	**<0.001**
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	**5.03**	**5.46**	**7.83**	**0.005**	1	1	0.32	0.57
	6-years lag of disturbed area (%)	**7.93**	**8.55**	**43.01**	**<0.001**				
	1-year lag of disturbed area (%)					**2.98**	**3.74**	**5.07**	**0.016**

Table S3. Results of generalized linear mixed models followed by multiple simultaneous comparisons of species numbers between undisturbed mature spruce forest (intact forest), salvage-logged disturbed forest (logged), and unlogged disturbed forest (unlogged), between one and eleven years following a major windstorm in the Bavarian Forest National Park.

Taxa	Year after disturbance	Simultaneous comparisons								
		salvaged–unsalvaged			salvaged–forest			forest–unsalvaged		
		Estimate	t-Value	p-Value	Estimate	t-Value	p-Value	Estimate	t-Value	p-Value
Bees and wasps	11	0.03 ± 0.108	0.274	0.784	**2.037 ± 0.208**	**9.793**	**>0.001**	**-2.008 ± 0.231**	**-8.686**	**>0.001**
Saproxylic beetles	1	0.08 ± 0.086	0.935	0.35						
	2	**-0.225 ± 0.085**	**-2.658**	**0.008**						
	3	**-0.336 ± 0.089**	**-3.766**	**>0.001**						
	4	-0.136 ± 0.09	-1.515	0.13						
	11	**0.267 ± 0.081**	**3.281**	**>0.001**	**0.329 ± 0.087**	**3.769**	**>0.001**	-0.062 ± 0.112	-0.552	0.581
Non-saproxylic beetles	11	**0.159 ± 0.062**	**2.566**	**0.01**	**0.567 ± 0.072**	**7.874**	**>0.001**	**-0.408 ± 0.085**	**-4.813**	**>0.001**
Epigeic Spiders	11	**0.143 ± 0.064**	**2.237**	**0.025**	**0.667 ± 0.082**	**8.115**	**>0.001**	**-0.524 ± 0.095**	**-5.539**	**>0.001**
Ants	11	**0.354 ± 0.137**	**2.582**	**0.01**	**1.318 ± 0.231**	**5.707**	**>0.001**	**-0.964 ± 0.248**	**-3.885**	**>0.001**
Wood-inhabiting fungi	1	-0.089 ± 0.248	-0.358	0.72						
	2	-0.195 ± 0.168	-1.158	0.247						
	3	-0.243 ± 0.143	-1.702	0.089						
	4	**-0.611 ± 0.132**	**-4.646**	**>0.001**						
	5	**-0.475 ± 0.127**	**-3.74**	**>0.001**						
	11	**-0.377 ± 0.169**	**-2.232**	**0.026**	0.271 ± 0.178	1.523	0.128	**-0.648 ± 0.191**	**-3.385**	**0.001**
Epigeic bryophytes	1	0.195 ± 0.144	1.353	0.176						
	2	0.04 ± 0.143	0.28	0.78						
	3	0.108 ± 0.14	0.771	0.441						
	4	0.121 ± 0.148	0.82	0.412						
	5	0.033 ± 0.156	0.214	0.831						
	11	**0.241 ± 0.123**	**1.961**	**0.05**	0.008 ± 0.146	0.055	0.956	0.233 ± 0.143	1.624	0.104
Epigeic lichens	1	-0.734 ± 0.768	-0.956	0.339						
	2	-1.006 ± 1.119	-0.899	0.369						
	3	-0.538 ± 0.709	-0.759	0.448						
	4	-1.841 ± 1.065	-1.728	0.084						
	5	-27.452 ± 639668.107	0	1						
	11	**1.042 ± 0.259**	**4.025**	**>0.001**	**0.736 ± 0.276**	**2.662**	**0.008**	0.306 ± 0.326	0.939	0.348
Epixylic bryophytes	1	0.223 ± 0.166	1.343	0.179						
	2	0.176 ± 0.159	1.107	0.268						
	3	0.262 ± 0.147	1.786	0.074						
	4	0.097 ± 0.146	0.665	0.506						
	5	0.073 ± 0.157	0.464	0.643						
	11	-0.071 ± 0.126	-0.561	0.575	-0.191 ± 0.136	-1.4	0.161	0.12 ± 0.151	0.795	0.426
Epixylic lichens	1	-0.229 ± 0.142	-1.611	0.107						
	2	**-0.292 ± 0.144**	**-2.031**	**0.042**						
	3	**-0.327 ± 0.136**	**-2.407**	**0.016**						
	4	-0.238 ± 0.137	-1.741	0.082						
	5	**-0.351 ± 0.138**	**-2.542**	**0.011**						
	11	**-0.372 ± 0.105**	**-3.554**	**>0.001**	**0.407 ± 0.112**	**3.643**	**>0.001**	**-0.779 ± 0.131**	**-5.953**	**>0.001**
Vascular plants	1	-0.008 ± 0.122	-0.065	0.948						
	2	0.037 ± 0.114	0.327	0.743						
	3	0.085 ± 0.112	0.757	0.449						
	4	0.037 ± 0.114	0.327	0.744						
	5	0.117 ± 0.11	1.065	0.287						
	11	0.073 ± 0.117	0.622	0.534	**0.382 ± 0.135**	**2.836**	**0.005**	**-0.31 ± 0.154**	**-2.011**	**0.044**
Birds	3	**-0.271 ± 0.135**	**-2.003**	**0.045**	**-0.364 ± 0.137**	**-2.655**	**0.008**	0.093 ± 0.128	0.727	0.467
	5	-0.079 ± 0.142	-0.561	0.575	**-0.646 ± 0.129**	**-4.986**	**>0.001**	**0.566 ± 0.126**	**4.482**	**>0.001**
	7	0.19 ± 0.121	1.568	0.117	-0.211 ± 0.113	-1.864	0.062	**0.401 ± 0.119**	**3.362**	**0.001**
	11	0.005 ± 0.108	0.047	0.962	**-0.21 ± 0.096**	**-2.178**	**0.029**	**0.215 ± 0.11**	**1.957**	**0.05**

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Chapter II

Estimating retention benchmarks for salvage logging to protect biodiversity

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Chapter II

Estimating retention benchmarks for salvage logging to protect biodiversity

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Abstract

Forests are increasingly affected by natural disturbances. Subsequent salvage logging, a widespread management practice conducted predominantly to recover economic capital, produces further disturbance and impacts biodiversity worldwide. Hence, naturally disturbed forests are among the most threatened habitats in the world, with consequences for their associated biodiversity. However, there are no evidence-based benchmarks for the proportion of area of naturally disturbed forests to be excluded from salvage logging to conserve biodiversity. We apply a mixed rarefaction/extrapolation approach to a global multi-taxa dataset from disturbed forests, including birds, plants, insects and fungi, to close this gap. We find that 75 ± 7% (mean ± SD) of a naturally disturbed area of a forest needs to be left unlogged to maintain 90% richness of its unique species, whereas retaining 50% of a naturally disturbed forest unlogged maintains 73 ± 12% of its unique species richness. These values do not change with the time elapsed since disturbance but vary considerably among taxonomic groups.

Keywords: Forest management, forest degradation, pest management, natural disturbance, wildfire, windstorm, bark beetle, biodiversity, climate change

Introduction

The world's forests are increasingly affected by natural disturbances, such as wildfires, windstorms or outbreaks of insect pests[1,2]. Increases in disturbance size, severity, and frequency are among the most severe impacts of climate change on forest ecosystems[3]. Many naturally disturbed forests are subsequently subjected to post-disturbance salvage logging, particularly in the temperate and boreal zones. Salvage logging is commonly justified to recover economic capital, reduce the risk of insect outbreaks, and decrease fire hazard[4]. It is sometimes also justified on the basis that it contributes to ecosystem recovery[5]. Salvage logging is conducted in all forest types, and is common even in areas that are otherwise excluded from logging, such as national parks[4]. By extracting timber and other tree biomass from large areas[5], salvage logging can impair ecosystem services[6] and affect the biodiversity of deadwood-dependent species[7]. Salvage logging can have more profound effects on biodiversity than natural disturbance or logging alone due to the additive and interacting effects of the two disturbances[8,9]. This has been exemplified by studies on changes in communities of birds[10–12] and vascular plants[13]. Currently, unlogged early-successional forests following stand-replacing natural disturbances are among the most uncommon habitats in many regions of the world[14]. Not surprisingly, species inhabiting these habitats have been targeted by conservation efforts. Examples include the black-backed woodpecker (*Picoides arcticus*) in the USA, largely restricted to burned forests and negatively affected by salvage logging[15,16]; the tree fern (*Cyathea australis*) in Australia, present on disturbed sites but virtually eliminated from areas subject to salvage logging[13]; and the white-spotted sawyer beetle (*Monochamus scutellatus*) in Canada, present after single natural disturbances, but absent from salvage-logged forests[8].

The increasing frequency and extent of natural disturbances have generated intense debates about the appropriateness of widespread, high-intensity salvage logging[17,18]. Hence, the retention of key structures in salvage logging operations (so-called biological legacies[19]), and the partial exclusion of naturally disturbed forests from salvage logging, are increasingly discussed as measures to halt the loss of forest biodiversity[7,20]. However, while benchmarks for a specific number of trees to be excluded from overall logging operations[21–23] are common measures in modern retention forestry, such benchmarks are rare for salvage logging of naturally disturbed forests[24]. Existing guidelines for managing disturbed forest stands often recommend the complete removal of disturbance-killed trees, for instance of all disturbance-affected Norway spruce (*Picea abies*) exceeding 10 m³ per ha in Finland[25]. By contrast, recent recommendations[26] advise the retention of all burned trees from fires larger then 100 ha in Catalonia, representing a minimum of 30% of all the burned area.

Estimating retention benchmarks for conserving biodiversity in the world's naturally disturbed forests has been hampered by several factors[26]. First, the effects of salvage logging on alpha diversity of species vary widely among forest ecosystems and taxonomic groups, ranging from severe species losses in deadwood-dependent and forest-dwelling groups to increases in those species groups that prefer open habitats[7]. Second, studies based on comparing alpha diversity between logged and unlogged forests disregard the fact that assemblages found in any two distinct habitat patches generally share a substantial fraction of species[27]. This regional diversity, which accumulates from compositional differences between local species assemblages (i.e., beta diversity), together with local alpha diversity, sums up to overall gamma diversity in a study landscape[28]. Hence, net changes in species richness can mask changes in community composition caused by species losses and replacements[29]. This may, in turn, lead to biased estimates of retention benchmarks.

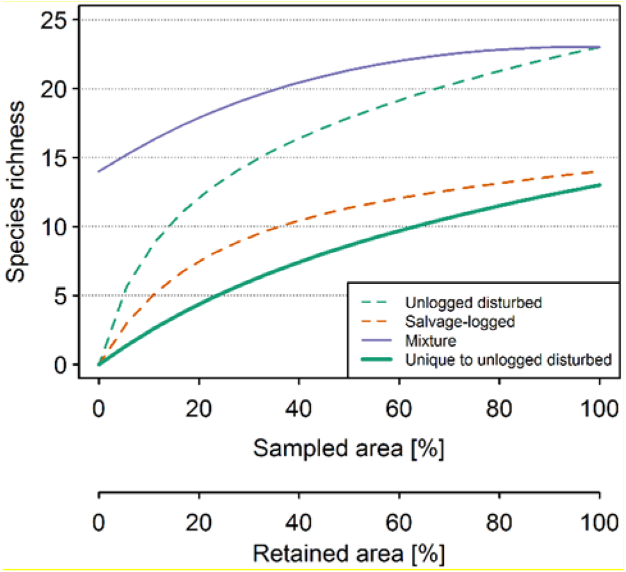

Figure 1 Hypothetical example of mixed rarefaction/extrapolation.

The example depicts species sampled in naturally disturbed but unlogged plots and naturally disturbed and salvage-logged plots. Unlogged plots (dashed green curve, upper x-axis) had a higher species richness rarefaction curve than salvage-logged plots (dashed orange curve, upper x-axis) across the proportion of sampled area. The solid purple curve represents the species richness for a given mixture of salvage-logged and unlogged plots. The richness of species that are unique to unlogged plots (solid green curve, lower x-axis; used in our analysis) increases with increasing proportion of unlogged disturbed plots in the mixture. Here only a mixture of two rarefaction curves is presented; see27 for a mixture including both rarefaction and extrapolation curves.

We use a recently developed statistical approach based on a mixture of rarefaction and extrapolation to forecast changes in species richness when naturally disturbed forests are subjected to a successive transformation by salvage logging[27]. Our approach utilizes a proportional mixture of two within-habitat rarefaction/extrapolation curves to analytically predict biodiversity changes in landscapes when a specified proportion of an original habitat is transformed. In our approach, the two within-habitat rarefaction/extrapolation curves (Fig. 1, dashed curves) depict, respectively, the estimated species-area relationships for unlogged disturbed plots and salvage-logged plots. When a proportion of an unlogged disturbed area is salvage logged, the between-habitat compositional difference can be incorporated into the proportional mixture model to predict the resulting diversity change due to salvage logging (Fig. 1, solid purple curve).

The mixed rarefaction/extrapolation curve allows us to assess species richness for any mixture of two habitat types[27] and to track the richness of species unique to unlogged, naturally disturbed forest (Fig. 1, bold green curve). These species are of high conservation interest and contribute greatly to community changes resulting from salvage logging[30]. We apply this statistical approach to a global dataset of studies with sampling units selected randomly from both naturally disturbed and salvage-logged areas to estimate logging benchmarks for naturally disturbed forests, namely a) the portion of naturally disturbed forest that must be spared from salvage logging to maintain 90% of the species richness associated with naturally disturbed and not salvage logged forest; and conversely b) the portion of species richness associated with naturally disturbed forest that remains when 50% of the area of a disturbed forest is salvage logged. Moreover, our statistical approach allows the quantification of species richness resulting from any portion of disturbed forest that is salvage logged.

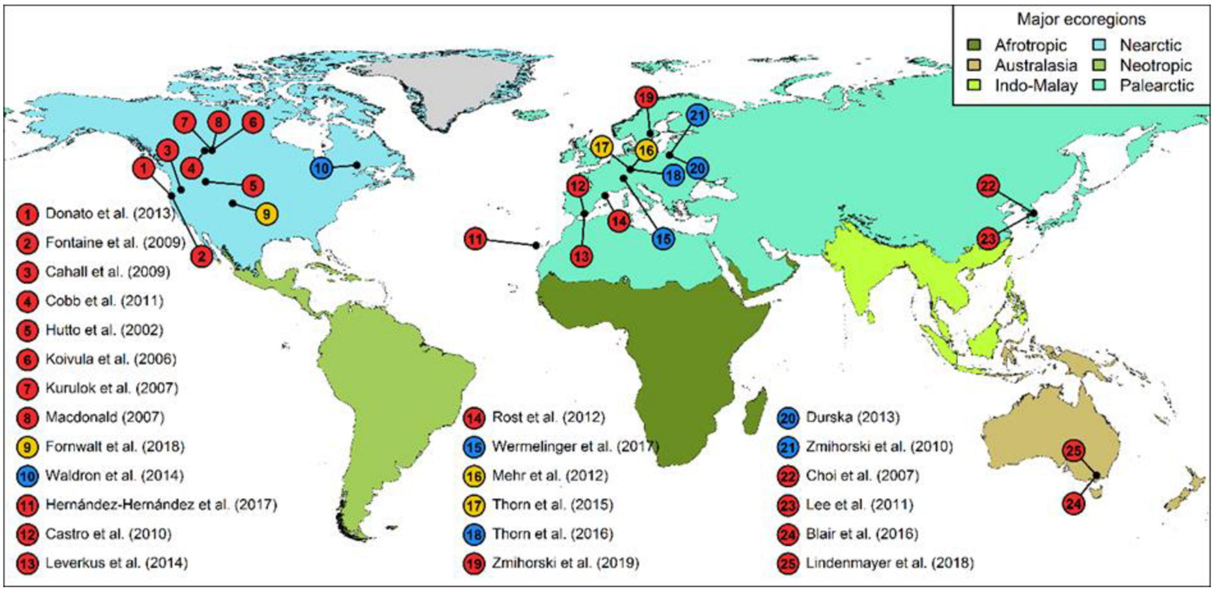

Figure 2 Location of studies included in the present analysis.
Each study provided species-by-plot abundance matrices for salvage-logged and unlogged, naturally disturbed forest plots. Disturbance types are indicated by different symbol colours (red: wildfires, blue: windstorms, yellow: insect outbreaks; see Supplementary Table 1 for details and references). Background colours indicate major terrestrial ecoregions[67].

We find that around 75% of a naturally disturbed area of a forest needs to be left unlogged to maintain 90% richness of its unique species, whereas retaining 50% of a disturbed forest unlogged maintains 73% of its unique species richness. These values, however, vary considerably among taxonomic groups, with deadwood-dependent (saproxylic) organisms, such as saproxylic beetles and wood-inhabiting fungi, generally requiring larger areas to be left unlogged than non-saproxylic taxa.

Results

Retention benchmarks

We analyzed 201 full species-by-plot abundance matrices of 17 different taxonomic groups derived from 25 studies (Fig. 2).

Averaging across all studies, our mixed rarefaction/extrapolation approach revealed that 75 ± 7% (mean ± SD) of a naturally disturbed area needs to be left unlogged to maintain 90% of the richness of species unique to it (Fig 3a). These values ranged from a mean of 72 ± 8% in the case of windstorms to 81 ± 4% and 87 ± 2% for wildfires and insect outbreaks, respectively, with SD ranges largely overlapping (Fig 3b). Saproxylic species groups needed, on average, larger areas to be retained (85 ± 3%) than non-saproxylic (72 ± 7%) species groups (Fig 3c).

Salvage logging on 50% of the disturbed forest area reduced the richness of species unique to disturbed, unlogged forest to an average of 73 ± 12% (Fig 3a). These values varied among disturbance types, and were lowest in insect-disturbed forests (reduction to 57 ± 5%), followed by burned forests (70 ± 9%), and wind-affected forests (75 ± 12%), with SD ranges largely overlapping (Fig 3b). Species richness appeared most susceptible to subsequent salvage logging in insect-disturbed forests, although data were scant for this disturbance type. Saproxylic species suffered more than other species groups if 50% of the overall area was salvage logged, with species richness dropping to 61 ± 8% compared to unlogged forests. By contrast, non-saproxylic species groups dropped only to 75 ± 11% (Fig 3c).

Differences among taxonomic groups

The estimated proportion of a naturally disturbed area that needs to be left unlogged to maintain species richness varied considerably among taxonomic groups (Fig. 4). Preserving 90% of species richness unique to disturbed, unlogged forest of several saproxylic taxa, such as wood-inhabiting fungi, saproxylic beetles, and epixylic lichens, required that 80 to 90% of disturbed forest be retained. In contrast, preserving 90% of species richness unique to disturbed, unlogged forest of several non-saproxylic taxa, such as true bugs, ground beetles, hoverflies, and epigeic spiders, required 50% to 65% retention (Fig. 4a). Salvage logging of 50% of a naturally disturbed forest led to a decrease of around 60% of the original species richness unique to disturbed forest for several saproxylic taxa, such as epixylic lichens and wood-inhabiting fungi, and for vascular plants. In contrast, for species groups with large numbers of non-saproxylic species such as true bugs, hoverflies, epigeic spiders, and ground beetles, the richness of species unique to disturbed forest remained between 80% and 90% after salvage logging 50% of the disturbed area (Fig. 4b).

Effect of time

Beta regression revealed that the proportion of a naturally disturbed area that needs to be left unlogged to maintain species richness did not change significantly with increasing time elapsed since disturbance (Fig. 5). This held true for both the retention area needed to maintain 90% of species unique to unlogged disturbed forest (estimated degrees of freedom of years since disturbance = 1.001, p-value = 0.11, adj. $r^2 = 0.75$), and the portion of species unique to unlogged naturally disturbed forest that remain after 50% of a given naturally disturbed area is salvage logged (estimated degrees of freedom of years since disturbance = 1.001, p-value = 0.13, adj. $r^2 = 0.75$).

Discussion

Using a global multi-taxa dataset, we estimate retention benchmarks needed for biodiversity conservation in naturally disturbed forests. We find that, across all investigated disturbance types, an average of 75% of the disturbed area needs to be unlogged to maintain 90% of the disturbed forest's unique species. The required areas to be left unlogged, however, varied considerably among taxonomic groups, with species groups associated with dead wood, such as saproxylic beetles and wood-inhabiting fungi, generally requiring larger portions (85%) than non-saproxylic taxa (72%). Our quantitative assessment has the additional advantage that it can be used to set any desired benchmark for biodiversity conservation. Our results also depict a relatively steep increase in species richness at the low part of portions of retained naturally disturbed area (Fig. 3).

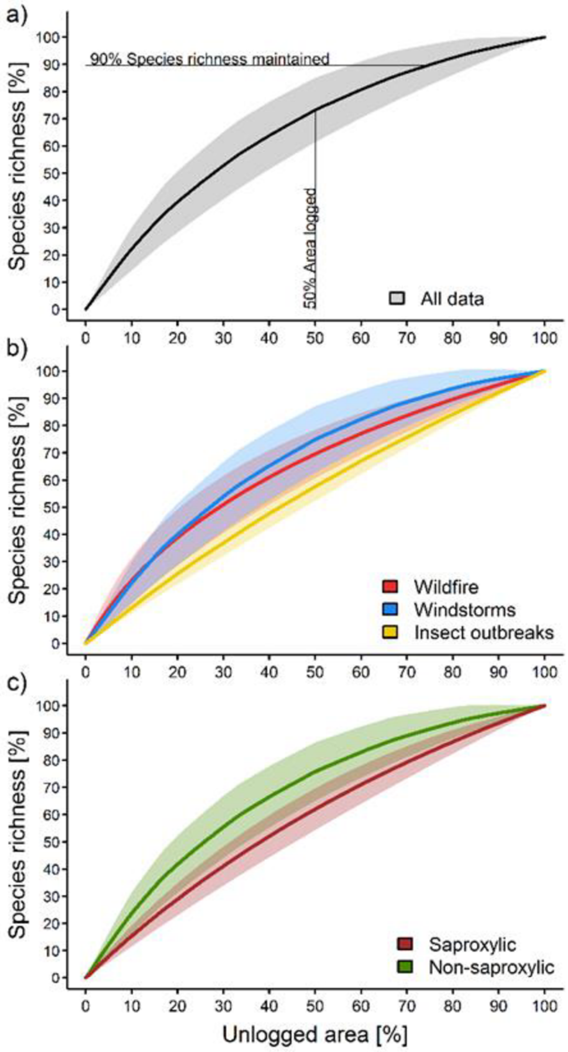

Figure 3 Response of species richness to different retention levels in salvage logging. Mean and standard deviation (shading) of richness of species unique to naturally disturbed, unlogged plots that would be maintained under varying portions of naturally disturbed forest excluded from salvage logging. The solid lines (means) are analogous to the solid green line from the hypothetical community in Fig. 1, indicating the mean response of 201 individual species matrices with a) all data pooled, b) datasets separated into different disturbance types, and c) datasets separated into saproxylic and non-saproxylic taxa. Source data are provided as a Source Data file.

Although comparisons with existing studies conducted under conventional logging schemes (i.e., without natural disturbances) are difficult, our results appear broadly similar to findings from work done in boreal forests of Finland[31]. There, wood amounts of 10 m³ and 50 m³ per ha were retained during clear-cut harvesting of pine-dominated stands of around 290 m³ per ha, corresponding to 3% and 17% of the original wood volume, respectively. Even the 3% retention level harboured many rare and red-listed saproxylic beetles, highlighting the importance of retaining even small amounts of wood[31]. Our results for saproxylic species are consistent with the conceptual framework developed by Fedrowitz *et al.*[32], which predicted an increase in forest species and a decline in open-habitat species (Fig. 4). This finding is not surprising because many positive effects of natural disturbances on the richness of forest specialists are related to an increase in available deadwood resources[7]. By contrast, taxonomic groups that typically reach high species richness in open areas needed, on average, lower portions of unlogged, disturbed area to be retained (Fig. 4); thus, epigeic spiders and ground beetles still maintained high proportions of species unique to unlogged forests even if 50% of the area was logged (Fig. 4b). In our data, these groups had high numbers of species in unlogged disturbed forests (Fig. 4, right column). Hence, the retention of smaller proportions of naturally disturbed forest might be sufficient to maintain a shady and moist microclimate, which can promote species associated with unlogged naturally disturbed forests (e.g., epigeic spiders and ground-dwelling beetles[33]). Finally, preservation of all species unique to unlogged naturally disturbed areas requires the retention of on average 100% of the disturbed area, whereas in some cases 100% richness could be reached with less than 100% retention (see standard deviation in Fig. 3a). This is particularly relevant for protected areas, where biodiversity protection is a primary aim[4].

Despite the small amount of data available from insect-affected forests, they appeared to need slightly higher amounts of retention area needed than forests subject to other kinds of natural disturbance to maintain the same amount of species richness (Fig. 3). This could arise from differences in the biological legacies left behind after different types of disturbance. In contrast to wildfires or windstorms, insect outbreaks typically leave behind intact ground, understory and midstory vegetation, as well as a longer-lasting vertical structure (i.e., insect-killed trees)[34], and thus logging likely results in a greater degree of environmental impact.

Our values for retention benchmarks did not change over time (Fig. 5), indicating that the importance of retained areas did not decrease or increase over the course of succession within the first ca. 20 years after salvage logging, which was the period best covered by our data. This time span is shorter than cutting cycles in most of the investigated forest types, which range between 60 and 120 years, but covers the most significant changes in tree cover and deadwood amount during the first 100 years. Differences in taxonomic, functional and phylogenetic diversity of bird communities sampled in unlogged disturbed plots and salvage-logged plots can persist or even increase over 17 years following fire and wind disturbance[11]. Similarly, a multi-taxa approach, including vascular plants, bryophytes, lichens, wood-inhabiting fungi, saproxylic beetles, and birds, revealed a limited change in dissimilarities between unlogged disturbed plots and salvage-logged plots over the first seven years of succession[30]. In that study, the remaining dissimilarities in communities were caused primarily by the presence or absence of rare species[30], quantified based on a similar statistical framework as in our study. Our results therefore imply that the positive effect of retention during salvage logging on biodiversity remains over the course of early succession. However, in some cases forests might need several centuries to regrow key structures – for instance, to recover the availability of tree hollows – so that the impacts of salvage logging on biodiversity can exceed 100 years[35].

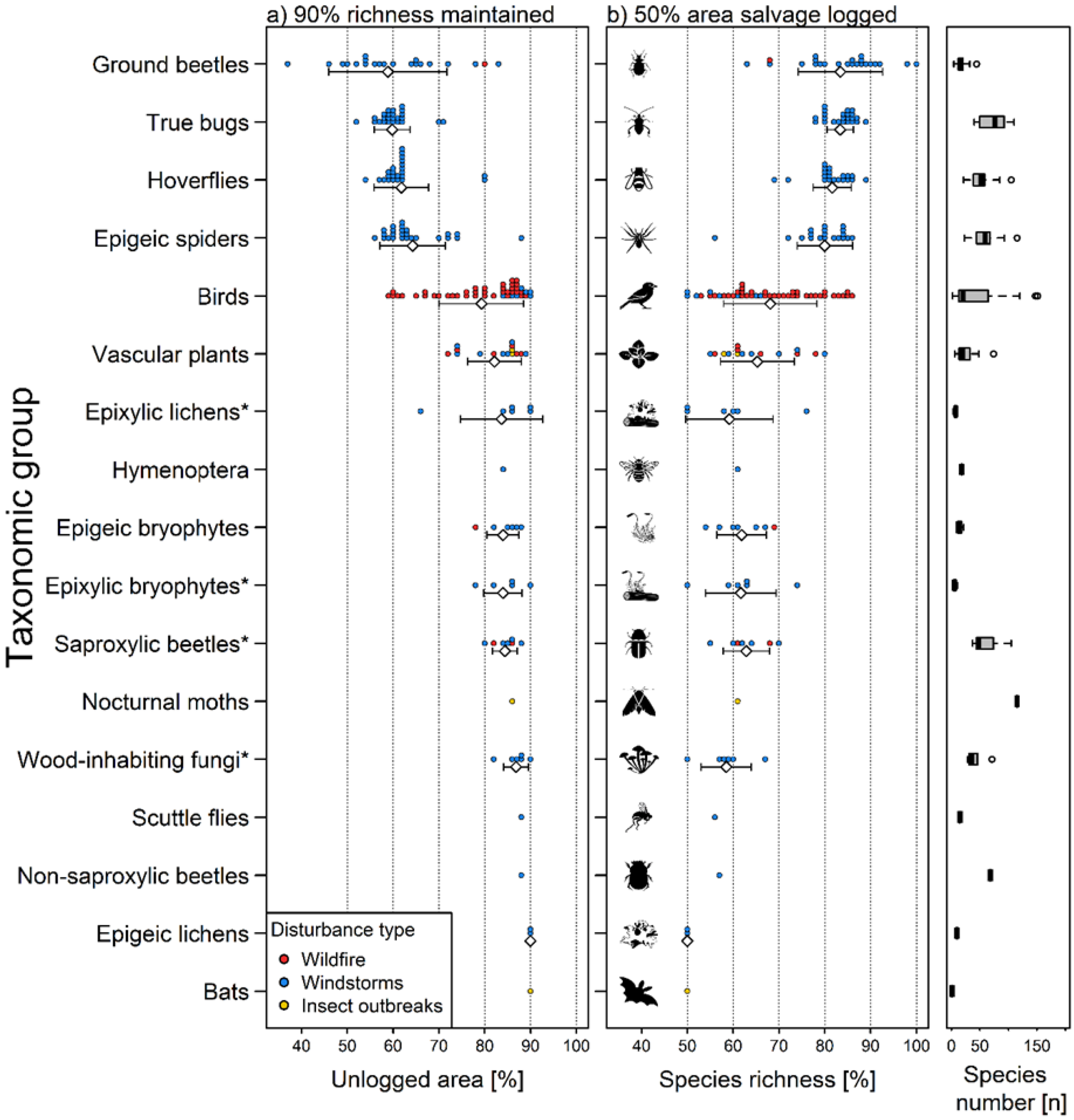

Figure 4 Estimated retention benchmarks for the assessed taxonomic groups

Distribution (dot histogram) and mean values (white diamonds) with corresponding standard deviation for: a) the retention area needed to maintain 90% of species unique to unlogged naturally disturbed forest; and b) the portion of species unique to unlogged naturally disturbed forest that would be maintained if 50% of the disturbed area was salvage logged. Saproxylic groups are marked with an asterisk. The right-hand box-whisker plots depict the median number of species unique to unlogged naturally disturbed plots (see Supplementary Table 1 for details) with lower and upper quartiles (box). Icons with permission from thenounproject.com. Source data are provided as a Source Data file.

Our statistical approach can be applied to any combination of two types of land use or habitats to reveal benchmarks for optimal enhancing overall biodiversity. This approach considers beta diversity by addressing the species unique to unlogged areas while simultaneously accounting for species that occur in both logged and unlogged areas within a landscape (Fig. 1). The detection of shared species is important, since many altered habitats typically share a large portion of species with the original habitat. Hence, comparisons based on alpha diversity alone might lead to biased benchmarks, since the net change in species richness can be small while the turnover between communities can be large[29]. This becomes particularly relevant for species unique to early-successional stages of naturally disturbed forests, where salvage logging can lead to marked changes in communities despite limited changes in alpha diversity of some taxonomic groups[7,34]. Contrarily, changes in species richness might be large while the turnover between communities in different habitat types is relatively small, i.e., a high number of species is shared[36]. Shared species can include species that utilize both forest types, for instance by roosting or breeding in unlogged disturbed forest and foraging in both unlogged and salvage-logged forests[37,38].

The benchmarks reported in our study are based on the number of species unique to unlogged, naturally disturbed forests. Hence, the overall increase or decrease in species richness with increasing extent of salvage logging depends both on the loss of species unique to unlogged naturally disturbed forests and on the simultaneous colonization of species typically found in salvage-logged forests[27]. Since shared species richness varies little across different proportional mixtures of two habitat types in statistical simulations[27], maintaining a minimum number of unique species from one of the two habitat types, i.e., unlogged naturally disturbed forest in our case, is approximately equivalent to maintaining a specific level of overall species richness. This pattern underlines the generalizability of our results, providing evidence-based benchmarks to protect biodiversity in naturally disturbed forests.

Methods

Database

We compiled a global database of species abundances in salvage-logged and unlogged naturally disturbed plots by extending two recent reviews (Fig. 2)[6,7]. The data compilation followed a systematic review protocol to ensure high quality standards in data selection[39]. We retained only those datasets that were based on field surveys and excluded modeling studies. In addition to the use of raw data from published studies, we extended three of the studies[40–42] by conducting additional surveys, adhering, in each case, to the original sampling design (Supplementary Table 1). All studies had to be conducted in forests where more than 75% of the trees had been affected by wildfires, insect outbreaks, or windstorms.

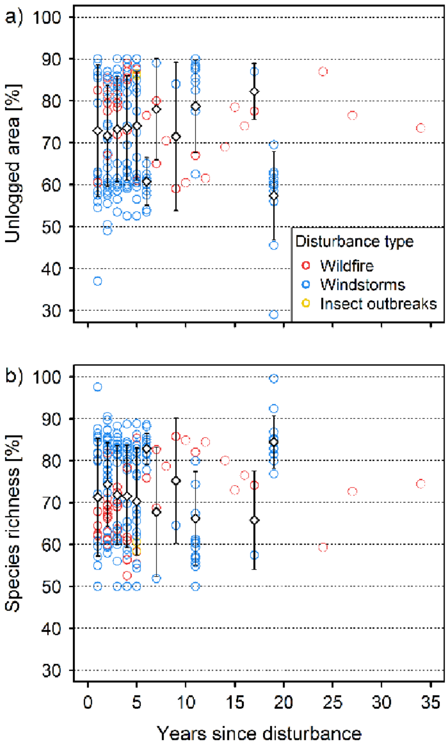

Figure 5 Response of retention benchmarks to time since disturbance.
Distribution (scatterplot) and annual mean values (white diamonds) with corresponding standard deviation across years for: a) the retention area needed to maintain 90% of species unique to unlogged naturally disturbed forest; and b) the portion of species unique to unlogged naturally disturbed forest that are maintained if 50% of the disturbed area is salvage logged. Source data are provided as a Source Data file.

Each study could provide multiple entries in our database given the number of investigated years and taxonomic groups. Study designs needed to provide comparisons between completely salvage-logged plots and completely unlogged, naturally disturbed reference plots, and both treatments had to be properly replicated[43]. The plots sampled in both treatments had to be located in the same forest affected by the same disturbance event, of similar size, and surveyed with the same sampling effort[7]. All study designs were checked for spatial autocorrelation between plots of the same treatment and excluded if necessary. Salvage logging had to have taken place in less than 36 months following the natural disturbance event.

The final database included full species-by-plot abundance matrices of bats[44], birds[12,40,51,41,42,45–50], ground beetles (Coleoptera, Carabidae)[52,53], dead-wood dependent (i.e., saproxylic) beetles[8,42], non-saproxylic beetles[42], Hymenoptera[42], epigeic spiders[53], epigeic and epixylic bryophytes[42,54], epigeic and epixylic lichens[42], hoverflies[53], nocturnal moths[55], scuttle flies[56], true bugs (Heteroptera)[53], wood-inhabiting fungi[42], and vascular plants[13,42,55,57–62]. We defined deadwood-dependent beetles, epixylic lichens, epixylic bryophytes, and wood-inhabiting fungi as saproxylic species groups. The database included the variables disturbance type, time elapsed since disturbance, and taxonomic group, which we used as covariates in our analysis. Our database consisted of 201 individual species matrices distributed across 17 taxonomic groups from studies conducted predominantly in temperate and boreal forests for up to 34 years following natural disturbance events (Fig. 2).

Data analysis

We used a statistical approach that extends classical rarefaction and extrapolation[63] towards a proportional mixture of two rarefaction/extrapolation curves derived from two distinct assemblages[27]. The analyses were conducted following the R code miNEXT (mixed iNterpolation/EXTrapolation, available at https://github.com/AnneChao).

The conventional species-area relationship describes the relationship between species richness and the sampling area using a parametric function (such as the Arrhenius model or Gleason model). However, a specified parametric function cannot be applied to all types of data. In our case, a within-habitat rarefaction/extrapolation curve represents a non-parametric species-area relationship estimated from the data themselves (Fig. 1, dashed curves). Estimated non-parametric species-area relationships can be applied to all types of data and compared across studies. Our proportional mixture enables the quantification of the between-habitat species compositional difference (i.e., beta diversity), which can be incorporated in the analysis to predict the resulting diversity change due to salvage logging[27].

Mixed rarefaction/extrapolation can either be applied to species abundances or species incidence/occurrence frequencies among plots. Furthermore, it can be applied even to unbalanced study designs, i.e., when the number of salvage-logged plots and disturbed unlogged plots differ. Our mixed rarefaction/extrapolation was based on T_1 plots surveyed in unlogged, disturbed forest and T_2 plots surveyed in corresponding salvaged logged forests. For all data, we treated the number of occurrences of each species among multiple plots as a proxy for the abundance of that species, as multiple incidence data are less sensitive than abundance data to possible clustering or aggregation of individuals[64]. When a proportion of unlogged disturbed plots (e.g., t plots) are salvage logged, it is equivalent to replacing these t plots by the same number of plots randomly selected from salvaged logged forests. Using a mixture of rarefaction and extrapolation, we can analytically retrieve the species richness of the mixed assemblage (Fig. 1).

Mixed rarefaction/extrapolation is independent of the underlying spatial arrangement of the study plots, i.e., it is based on comparisons of plots randomly selected from any location of a study design and is independent of plot size and the number of plots within a respective study, as long as all plots within a study are of similar sizes. Our benchmarks are hence independent of the spatial arrangement of the underlying study plots[27]. This is particularly important as detailed information about the size of a disturbed area for each study year was not available. Mixed rarefaction/extrapolation also provides species composition information, i.e., shared species richness and the richness of species that are unique to either unlogged, disturbed or salvage-logged plots under any proportion of the mixture[27]. In our synthesis, we focused on the richness of species unique to unlogged, disturbed forests (Fig. 1). Mixed rarefaction/extrapolation allows for the estimation of the number of plots associated with a specific level of species richness that is unique to unlogged, disturbed plots. The proportion of these plots can subsequently be used as a proxy for the proportion of area that needs to be excluded from salvage logging[27]. Using mixed rarefaction/extrapolation, we estimated retention areas for different taxonomic groups and disturbance types to identify benchmarks of group-specific salvage-logging retention.

Finally, we fitted beta regressions by means of the function *gam* with family *betar* in the R-package *mgcv*[65] to test the effect of time since disturbance on retention benchmarks. For this purpose, we selected the year since disturbance as smooth term to account for possible non-linear relationships[11]. Furthermore, we controlled for study identity, taxonomic group and disturbance type via additional predictors.

Data Availability

The data collected in the Bavarian Forest National Park may be found in the BIOtime (http://biotime.st-andrews.ac.uk/downloadArea.php) database[66]. All other original data underlying our analyses can be made available by the respective co-authors upon reasonable request. Source data are provided with this paper.

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Author contributions

ST, JM and ABL designed the study and developed the idea. AC and ST analysed the data. ST wrote the first draft of the manuscript. All authors contributed significantly to revisions and provided data.

Competing interests

The authors declare no competing interests.

Additional information

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Supplementary Information File

Estimating retention benchmarks for salvage logging to protect biodiversity

Thorn et al.

Supplementary Table 1. Summary of the data included in the study.

Note that plot sizes refer to the size of plots given the respective references. Note that ‘not applicable’ (n.a.) is given, if the respective surveys were conducted on a standardized number of deadwood objects (e.g. wood-inhabiting fungi) or used insect traps, where the range cannot be standardized (e.g. flight-interception traps, pitfall-traps).

Taxonomic group	Location	Disturbance	Number of studied years	First studied year after disturbance	Last studied year after disturbance	Number of disturbed unlogged plots	Number of salvage-logged plots	Single plot size [ha]	Ref.
Vascular plants	Oregon, USA	Fire	1	4	4	80	85	0.0013-0.09	1
Birds	Oregon, USA	Fire	1	4	4	64	58	1	2
Birds	Oregon, USA	Fire	2	1	2	5	5	2.01	3
^{S}Saproxylic beetles	Alberta, Canada	Fire	2	1	2	6	6	n.a.	4
Birds	Montana, USA	Fire	18	1	27	6–2410	8–651	3.14	5*
Ground beetles	Alberta, Canada	Fire	1	2	2	48	48	n.a.	6
Vascular plants	Alberta, Canada	Fire	2	2	34	38–40	40–45	0.0004	7
Vascular plants	Alberta, Canada	Fire	1	2	2	13	14	0.0004	8
Vascular plants	Colorado, USA	Insect outbreak	1	2	2	5	5	0.005	9
Vascular plants	Quebec, Canada	Wind	1	4	4	12	24	0.0004	10
Epigeic bryophytes	Canary Islands, Spain	Fire	1	3	3	86^{m}	73^{m}	0.01	11
Birds	Sierra Nevada, Spain	Fire	2	2	3	9	18	2.7	12
Vascular plants	Sierra Nevada, Spain	Fire	1	2	2	9	9	2.7	13
Birds	Catalonia, Spain	Fire	2	2	3	15–42	16–43	3.7	14
Epigeic spiders	Switzerland	Wind	7	1	19	8–13	8–10	n.a.	15
Ground beetles	Switzerland	Wind	7	1	19	8–13	8–10	n.a.	15
True bugs	Switzerland	Wind	7	1	19	6–8	6	n.a.	15
Hoverflies	Switzerland	Wind	7	1	19	6–8	6	n.a.	15
Bats	Bavarian Forest National Park, Germany	Insect outbreak	1	5	5	8	8	n.a.	16
Vascular plants	Bavarian Forest National Park, Germany	Insect outbreak	1	5	5	8	8	0.785	17
Nocturnal moths	Bavarian Forest National Park, Germany	Insect outbreak	1	5	5	8	8	n.a.	17
Vascular plants	Bavarian Forest National Park, Germany	Wind	7	1	11	23–24	19–20	0.02	18*
Epigeic bryophytes	Bavarian Forest National Park, Germany	Wind	6	1	11	24–25	24	0.02	18*
^{S}Epixylic bryophytes	Bavarian Forest National Park, Germany	Wind	6	1	11	19	18–19	n.a.	18*
^{S}Epigeic lichens	Bavarian Forest National Park, Germany	Wind	6	1	11	3–16	2–23	0.02	18*
^{S}Epixylic lichens	Bavarian Forest National Park, Germany	Wind	6	1	11	19	18–19	n.a.	18*

^{S}Wood-inhabiting fungi	Bavarian Forest National Park, Germany	Wind	6	1	11	19	11–19	n.a.	18*
^{S}Saproxylic beetles	Bavarian Forest National Park, Germany	Wind	5	1	11	22	22	n.a.	18*
Birds	Bavarian Forest National Park, Germany	Wind	4	1	11	20–21	20–32	0.785	18*
Hymenoptera	Bavarian Forest National Park, Germany	Wind	1	11	11	22	22	n.a.	18*
Non-saproxylic beetles	Bavarian Forest National Park, Germany	Wind	1	11	11	22	22	n.a.	18*
Birds	Sweden	Fire	4	1	4	69	40	0.785	19*
Scuttle flies	Poland	Wind	1	3	3	6	5	n.a.	20
Birds	Poland	Wind	3	5	11	38–49	54–57	3.14	21*
Birds	South Korea	Fire	1	5	5	19	19	1	22
Birds	South Korea	Fire	2	7	8	10–14	10–14	10	23
Birds	Victoria, Australia	Fire	6	1	7	18-42	24-42	0.785	24
Vascular plants	Victoria, Australia	Fire	1	2	2	28	28	0.03	25

^{S} indicates saproxylic species groups

^{m} indicates that microplots where used for the analyses

* The study dataset was expanded by adding unpublished data

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Chapter III

Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging

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Chapter III

Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging

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Keywords

temperate forests; disturbance; bees and wasps; saproxylic beetles; deadwood amount; canopy gaps

Abstract

Forests are increasingly affected by natural disturbances like fires, insect outbreaks, and windstorms. Such disturbances are commonly followed by salvage logging. Disturbance and salvage logging affect biodiversity by altering microclimate, habitat structure, and deadwood amount. To mitigate possible negative effects of salvage logging on biodiversity, ecologists often recommend the retention of disturbance-created structures. However, the mechanisms through which retained structures affect biodiversity remain largely unknown. We analysed 9,602 individuals of saproxylic beetles belonging to 268 species and 3,172 individuals of aculeate Hymenoptera belonging to 68 species of cavity-nesters and 126 species of non-cavity-nesters over two years in a wind-disturbed beech forests with various intensity of salvage logging. We quantified the relative importance of canopy openness and deadwood amount. Our final dataset consisted of 268 saproxylic beetle species and 194 species of aculeate Hymenoptera out of which 68 were cavity-nesters and 126 non cavity-nesters. Generalized linear mixed effect models showed the lowest number of Hymenoptera and beetle species in undisturbed forest. Permutational analysis of variance revealed that treatment and canopy openness drive community composition of both taxa. Increased canopy openness was the main factor positively affecting numbers of species of aculeate Hymenoptera and saproxylic beetles in the first two years after the disturbance. Deadwood amount only affected community composition of saproxylic beetles. However, gamma diversity and community composition of saproxylic beetles indicated that disturbed and extensively logged plots resembled disturbed unlogged plots rather than disturbed and intensively logged plots. Our findings suggest that at least some timber might be extracted from disturbed areas, without major losses of biodiversity of saproxylic beetles and aculeate Hymenoptera.

1. Introduction

Natural forest disturbances, including wildfires, insect outbreaks, and windstorms increasingly affect forests around the world (Kurz *et al.*, 2008; Seidl *et al.*, 2014). As a result, the amount of forests subjected to post-disturbance 'salvage' logging, i.e. the removal of disturbance-affected trees, has simultaneously increased (Lindenmayer and Noss, 2006; Leverkus *et al.*, 2018, 2021). Natural disturbances alter forest structures, including an increase in deadwood availability and increase in canopy openness (Frolking *et al.*, 2009; Cobb *et al.*, 2011; Swanson *et al.*, 2011). This, in turn, creates habitats for light-demanding species and species that require greater amounts of deadwood, or a combination of both (Stevens *et al.*, 2015; Wermelinger *et al.*, 2017). For instance, saproxylic insects, beetles in particular, benefit from forest disturbance and the increased availability of deadwood of various types (Lachat *et al.*, 2012; Bogusch *et al.*, 2015; Thorn, Bußler, *et al.*, 2016; Eckelt *et al.*, 2018). Additionally, cavity-nesting aculeate Hymenoptera can benefit from increased amounts of deadwood, while cavity and ground-nesting hymenopteran species, as well as saproxylic beetles, benefit from increase in canopy openness. Furthermore, easier access to bare soil on disturbed patches benefits ground-nesting hymenopteran species (Grundel *et al.*, 2010; Williams, Crone, T'ai H. Roulston, *et al.*, 2010; Koch Widerberg *et al.*, 2012; Horák and Rébl, 2013; Wermelinger *et al.*, 2017).

Legal requirements demand that salvage logging takes place following natural disturbances in many cases (Müller *et al.*, 2019). Due to the removal of deadwood, salvage logging leads to a reduction of resources for saproxylic organisms (Thorn *et al.*, 2018) and increases canopy openness (Thorn *et al.*, 2018; Leverkus *et al.*, 2020, 2021). Thus, salvage logging may benefit organisms adapted to open habitats, such as ground-nesting bees, due to an increase in the availability of bare soil (Taki *et al.*, 2013; Galbraith *et al.*, 2019), while the effects on deadwood-dependent organisms, such as saproxylic beetles or cavity-nesting Hymenoptera, may be negative (Thorn, Chao, *et al.*, 2020). To mitigate the negative effects of salvage logging on biodiversity, ecologists and conservationists increasingly call for ecologically sustainable strategies in the management of disturbed forests (Lindenmayer, Thorn and Banks, 2017).

A simple way to maintain natural processes and biodiversity associated with disturbed forests is the partial or complete exclusion of disturbed forest patches from salvage logging (Thorn, Chao, *et al.*, 2020). However, legal requirements often prohibit the complete set-aside of disturbed stands, particularly if salvage logging is required for pest control. Hence, integrated approaches, which combine the requirements of nature conservation, pest control and the provision of timber are needed (Schmiegelow *et al.*, 2006; Müller *et al.*, 2019). A widespread integrated approach to minimize the negative impacts of conventional green-tree logging is the retention of ecological key features (Lindenmayer *et al.*, 2012; Sebek *et al.*, 2016). In disturbed forests, biological legacies (Franklin *et al.*, 2000) are key features following disturbances and include surviving trees, snags, downed woody debris, undisturbed understory or root plates (Swanson *et al.*, 2011). However, while there are studies directed towards a retention of biological legacies in otherwise salvage-logged stands (Rudolphi, Jönsson and Gustafsson, 2014; Leverkus *et al.*, 2018; Augustynczik *et al.*, 2020), empirical evidence of the effects of different levels of retention on biodiversity remains scarce. This is mostly because the rapid management response to natural disturbances often impedes retention (Lindenmayer *et al.*, 2004). Yet, the relative importance of canopy openness and deadwood amount in determining biodiversity response to post-disturbance management remains unclear.

Saproxylic beetles are a diverse group of insects often used as indicators of woodland quality (Thorn, Seibold, *et al.*, 2020). In particular, deadwood amount and microclimate are key factors influencing communities of saproxylic beetles (Lachat *et al.*, 2012, 2013; Horak *et al.*, 2014; Seibold *et al.*, 2016; Lettenmaier *et al.*, 2022). However, the relative importance of deadwood amount versus canopy openness on saproxylic beetle communities remains unclear. Aculeate Hymenoptera are typically associated with open habitats, such as meadows, forest edges and forest openings (Proctor *et al.*, 2012; Bennett, Gensler and Cahill, 2014; da Rocha-

Filho *et al.*, 2017). Hymenopterans are limited by nesting opportunities with about one third being nest parasites of other Hymenoptera (and as such are limited by the nesting of their host). About half of all species nest in ground and as such benefit from the general openness of habitat as well as bare soil availability (Michener, 2007; Grundel *et al.*, 2010; Williams, Crone, T. H. Roulston, *et al.*, 2010). Approximately one fifth of European hymenopteran species nest in various cavities and about 85% of cavity nesters nest in wood (Bogusch and Horák, 2018). Such cavity nesters and associated nest parasites benefit from forest disturbance due to an increase in potential nesting sites coupled with an increase in canopy openness (Morato and Martins, 2006; Tylianakis *et al.*, 2006; Taki *et al.*, 2008; Lettow *et al.*, 2018).

Here, we investigated changes in the diversity of saproxylic beetles and aculeate Hymenoptera following windstorm disturbance and salvage logging in temperate deciduous forests. We used four experimental treatments, i.e. undisturbed forest, disturbed unlogged forest, disturbed extensively logged and disturbed intensively logged stands, in order to quantify the effects of disturbance and subsequent management, as well as openness and deadwood amount, on the diversity of saproxylic beetles, cavity-nesting Hymenoptera and non-cavity-nesting Hymenoptera. We hypothesised that i) higher canopy openness increases species richness of all focal insect groups; ii) increased amount of deadwood increases the species richness of saproxylic beetles and cavity nesting Hymenoptera; iii) communities of all studied insect groups differ between undisturbed forest and disturbed plots; and iv) within the disturbed forests, richness and community composition is affected by logging intensity. Furthermore, we quantified differences between the two sampling years and derived management recommendations based on the above-described hypotheses.

2. Methods

2.1. Study area and experimental design

The study area is located in the forests of the northern Steigerwald, Bavaria, Germany (N 49°50', E 10°29') which are managed by the Bavarian State Forest Enterprise, Ebrach (Kraus and Mergner, 2020) on an area of approximately 16,500 ha. According to Doerfler *et al.*, 2017, these forests in 2010 were characterized by a large proportion of broadleaved trees, mainly *Fagus sylvatica* 39% (basal area: 18,578 m^2/ha), *Quercus* spp. 21% (basal area: 6,599 m^2/ha), and 12% other deciduous as well as 27% coniferous trees, mainly *Pinus sylvestris* and *Picea abies.* Average stand age was 92 years. Stands are managed as even-aged high forests with interventions about every ten years including the extraction of single trees and selective logging with the retention of old trees to promote rejuvenation (Doerfler *et al.*, 2017). On 24th September 2018, the storm „Fabienne" affected around 40,000 m^3 of timber, mostly from broadleaved trees. Our plots were established in four extensive areas with more than 75% canopy mortality i.e. 75% of tree layer removed by the storm, hereafter called experimental blocks (Fig. 1). Each block contained an undamaged, even-aged stand, managed by selective logging (undisturbed forest), a stand damaged by the storm without any intervention (disturbed unlogged), a forest damaged by the storm from which only the main trunks, up to the first larger branches, were removed (disturbed extensively logged) (Doerfler *et al.*, 2017), and a storm-damaged stand from which all timber larger than 7 cm in diameter was removed with the exception of tree stumps (disturbed intensively logged). This way, besides undisturbed forest, we had three disturbed treatments with three levels of logging intensity. The plot size was around 1.1 ha on average (min. 0.81 ha, max. 3.39 ha), while the largest block contained two sets of experimental plots (Fig. 1, block a). After the experimental treatment, plots were left to natural succession. Therefore, there were four blocks with 20 research plots altogether. In each plot, we collected data on deadwood amount, canopy openness, and species numbers of saproxylic beetles and aculeate Hymenoptera.

2.2. Insect sampling

Saproxylic beetles and aculeate Hymenoptera were sampled with two flight-interception traps placed at the centre of each plot in 2019 and 2020. Flight-interception traps consisted of a crossed pair of transparent plastic shields with size of 40 cm × 60 cm. Traps were exposed from April to September and emptied monthly. The classification of saproxylic beetles followed Schmidl & Bußler (2004). Saproxylic beetles were identified according to Freude, Harde and Lohse (1965). Hymenoptera were identified and split into cavity and non-cavity-nesting species based on available literature (Macek *et al.*, 2010) as large part of cavity-nesting species utilize or very likely utilize deadwood (Bogusch and Horák, 2018). Hymenopteran nest parasites were added to these groups based on the nesting strategy of their most common hosts as the nesting substrate requirement of the parasite is the same as that of its host (Dollfuss, 1992; Amiet, 1996; Amiet *et al.*, 1999, 2004; Amiet, Müller and Neumeyer, 2001, 2007; Schmid-Egger, 2002; Dvořák and Roberts, 2006; Bogusch and Straka, 2012).

2.3. Environmental parameters

Deadwood amount was measured in three subplots per plot, each 1000 m² in size. Here, all deadwood objects (logs, stumps, high stumps, tree crowns) larger than 7 cm in diameter were inventoried (modified after Robin and Brang, 2009) and volumes were calculated according to Kramer and Akça (2008). The subplots were distributed across the respective plots to cover the local variance in deadwood amount, having no overlap to each other and covering the spatial extent of the plot. Recorded deadwood was classified into five different decay stages (Kaufmann *et al.*, 2005) of which only the first two were included in the analysis, i.e. we excluded living trees and all deadwood that has not been created by the windstorm or subsequent logging activities.

Canopy openness was measured near the plot centre between the traps using a Faro Focus M70 (Faro Technologies Inc, Lake Mary, USA) terrestrial laser scanner (Zheng, Moskal and

Kim, 2013). Our measure of canopy openness is the percentage of vegetation cover in an upward facing canopy image simulated for the exact position of the scanner, i.e. 1.3 m above ground. Thereby, the viewing angle is restricted to a 60° opening angle (upside-down cone) to consider only nearby canopy. This measure proved useful in earlier studies, e.g. as a predictor of the stand microclimatic conditions (Ehbrecht *et al.*, 2019). Scanning was performed on 15th September 2020 during dry and calm weather conditions and the scanner was set to operate with an angular resolution of 0.035° for a field of view of 300 degrees vertically and 360 degrees horizontally.

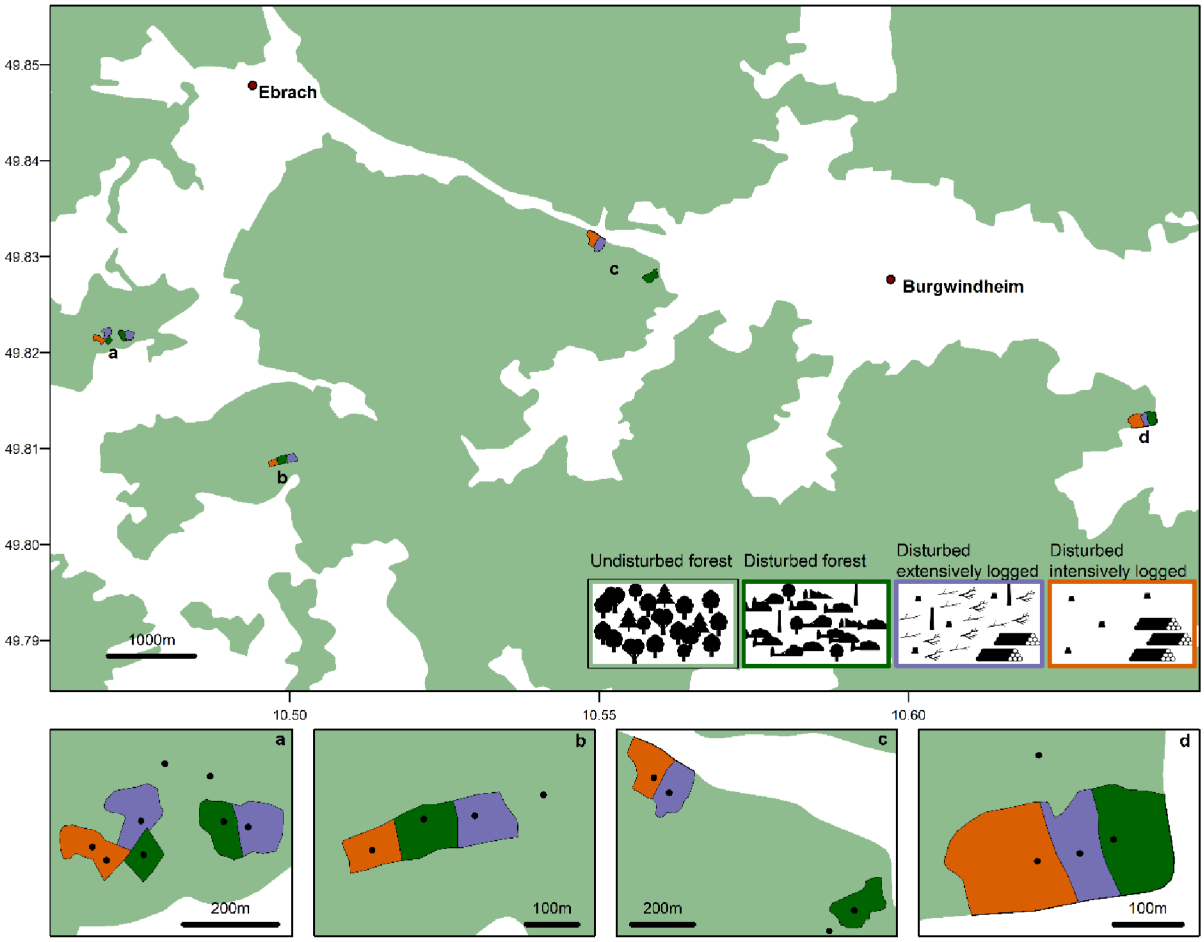

Figure 1: Spatial arrangement of the study plots within the four experimental blocks in Ebrach forest district, Steigerwald, Bavaria, Germany. Black dots depict centres in between the two flight-interception traps.

2.4. Data analysis

All data analyses were carried out in R version 4.0.2 (R Core Team, 2020). Prior to statistical analysis, all samples were pooled to the trap level within each year, so our dataset consisted of 80 data points (5 sites, 4 treatments, 2 traps per treatment in 2 sampling years). We controlled for correlation between deadwood volume and canopy openness and their differences among the treatments prior to further analyses.

To test the effect of the treatment (undisturbed forest, disturbed unlogged, disturbed extensively logged, disturbed intensively logged) and then separately deadwood amount and canopy openness on the number of species (alpha diversity) of each group of insects, we fitted generalized linear mixed models for Poisson-distributed data (Bolker *et al.*, 2009) using the 'lme4' package (Bates *et al.*, 2015). First, we fitted a model with treatment as an explanatory factor variable, sampling year as a covariate and the number of species as a response variable. We added the experimental block and plot as a random effect (1|block/plot) to account for the nested design (Fig. 1). We compared this model with a simplified model including only the sampling year as a covariate to assess the significance of the treatment. Pairwise comparisons between treatment levels were further performed by means of multiple comparisons for parametric models with simultaneous adjustment of p-values (stepwise-method), provided by the function 'glht' from 'multcomp' R package (Hothorn, Bretz and Westfall, 2008). Second, we fitted a model with deadwood amount, canopy openness, and their interaction as explanatory variables and sampling year as a covariate. This model was fitted in order to reveal which of these continuous variables has a major effect on the number of species, as the treatment levels represented categories with combined effects of the two variables.

To compare cumulative numbers of species (gamma diversity) between the different treatments we used interpolation and extrapolation approaches based on Hill numbers (Chao *et al.*, 2014) implemented in the 'iNEXT' R package (Hsieh & Chao, 2016). Here, species accumulation curves with confidence bands based on 50 bootstrap replicates allow the comparison of observed gamma diversity standardized by species density. We used different levels of q to show the effect of experimental treatments on numbers of species (q=0), Shannon diversity (q=1), and Simpson diversity (q=2). Selecting different values of q changes the sensitivity of the analyses to species relative abundances, increasing from rare (q=0), to common (q=1), to dominant (q=2) species (Chao *et al.*, 2021).

To analyse the effects of the experimental treatment and sampling year on species composition, we used permutational multivariate analysis of variance (Legendre and Anderson, 1999) provided by the 'vegan' package (Oksanen *et al.*, 2016). We selected the treatment and year as explanatory variables, permuted within experimental blocks. Bray-Curtis distances were used to derive the associated resemblance matrices of species data pooled on plot level. The p-values obtained in multiple permutational multivariate analysis were adjusted by means of Bonferroni correction (Benjamini and Hochberg, 1995). The dissimilarities in the studied insect communities were visualized by means of non-metric multidimensional scaling (NMDS) (Minchin, 1987). The same approach was also used to analyse the effect of canopy openness and deadwood amount together with sampling year. We calculated similarity percentages to reveal species, which contribute most to the differences between treatments by means of the function 'simper' provided by the 'vegan' package (Clarke, 1993).

3. Results

In total, we identified 9,602 individuals of saproxylic beetles belonging to 268 species and 3,172 individuals of aculeate Hymenoptera belonging to 68 species of cavity-nesters and 126 species of non cavity-nesters (Supplementary material Table A.1, Table A.2, and Table A.3). The median deadwood volume per hectare was 19.72 m^3, 151.53 m^3, 84.76 m^3, and 19.97 m^3 for undisturbed, disturbed unlogged, disturbed extensively logged and disturbed intensively logged plots, respectively. The deadwood amount was significantly higher on disturbed unlogged and disturbed extensively logged plots compared to undisturbed forest and disturbed intensively logged plots ($\chi^2_{(3)}$=156, P<0.001) (Fig. 2). Canopy openness was also different among the treatments ($\chi^2_{(3)}$=120.8, P<0.001), median canopy openness increased from 7.67%, to 61.33%, to 73.87% to 97.09% for undisturbed, disturbed unlogged, disturbed extensively logged and disturbed intensively logged plots, respectively (Fig. 2). The two variables were not correlated (Pearson correlation coefficient = -0.084).

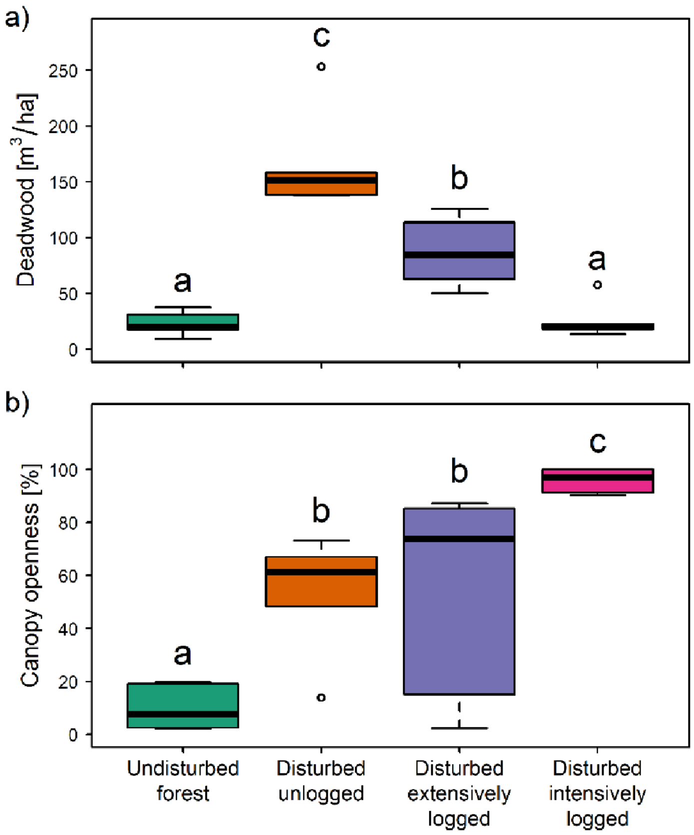

Figure 2: a) Deadwood volume (m^3/ha) and b) canopy openness (%) measured by terrestrial laser scanning across treatments in wind-disturbed beech forests. Different letters above boxplots indicate statistically significant differences (P<0.05).

There were significant differences in numbers of species among the treatments (non-cavity-nesting Hymenoptera: $\chi^2_{(3)}$=26.41, P<0.0001; cavity-nesting Hymenoptera: $\chi^2_{(3)}$=16.35, P=0.0009; saproxylic beetles: $\chi^2_{(3)}$=16.25, P=0.001) (Table 1, Fig. 3). Number of species of all studied insect groups was lowest in the undisturbed forest and then increased with increasing post-disturbance logging intensity (the disturbed intensively logged plots having the highest numbers), with significant difference between undisturbed forest and intensively logged plots for all the groups (Fig. 3). In Hymenoptera, all the disturbed plots were significantly richer than the undisturbed forest (Fig. 3a, Fig. 3b), for saproxylic beetles, the difference was found between the undisturbed forest and disturbed logged treatments (both extensive and intensive) (Fig. 3c). Statistical details of pairwise comparisons are given in the Supplementary material (Table A.4). When the effect of deadwood amount, canopy openness, and their interaction was analysed, the model showed a significant positive effect of openness on the number of species of all studied insect groups (Table 2), but no effect of deadwood amount or its interaction with openness. In both models, the effect of the sampling year (covariate) was significant for both groups of Hymenoptera (numbers increased in the second year), but not for saproxylic beetles (Table 1, Table 2).

Plot-based rarefaction-extrapolation curves showed a relatively low species accumulation rate at the sampling effort of the study, suggesting sufficient number of traps, and revealed the lowest cumulative number of species (gamma diversity) of all studied groups in the undisturbed forests (Fig. 4 for the q=0 setting). The pattern in the cumulative numbers resembled the one in alpha diversity: in Hymenoptera we found higher numbers in all disturbed treatments (logged and unlogged) than in the undisturbed forests, in saproxylic beetles, the numbers increased in disturbed forests with increasing logging intensity, the highest numbers were observed in the disturbed intensively logged plots (Fig. 4c). The results were similar for q=1 and q=2 (see Supplementary material Fig. A.1 and Fig. A.2).

Table 1: Coefficient estimates of the generalized linear mixed models with Poisson error distribution testing the effect of sampling year (Year, with levels 2019 and 2020) and treatment (with levels: Undisturbed forest, Disturbed unlogged, Disturbed extensively logged, Disturbed intensively logged) on the number of species of aculeate Hymenoptera and saproxylic beetles per plot. Significant parameters are highlighted in bold.

Group	Model parameter	Estimate	Standard error	z value	P value
Non-cavity-nesting Hymenoptera	**Intercept (Undisturbed forest-2019)**	**1.013**	**0.258**	**3.93**	**<0.0001**
	Year-2020	**0.436**	**0.067**	**6.51**	**<0.0001**
	Disturbed unlogged	**1.115**	**0.205**	**5.43**	**<0.0001**
	Disturbed extensively logged	**1.030**	**0.207**	**4.99**	**<0.0001**
	Disturbed intensively logged	**1.574**	**0.201**	**7.81**	**<0.0001**
Cavity-nesting Hymenoptera	Intercept (Undisturbed forest-2019)	-0.561	0.384	-1.46	0.143
	Year-2020	**0.416**	**0.132**	**3.15**	**0.002**
	Disturbed unlogged	**1.320**	**0.392**	**3.37**	**0.0007**
	Disturbed extensively logged	**1.316**	**0.392**	**3.36**	**0.0008**
	Disturbed intensively logged	**1.774**	**0.387**	**4.58**	**<0.0001**
Saproxylic beetles	**Intercept (Undisturbed forest-2019)**	**2.992**	**0.117**	**25.52**	**<0.0001**
	Year-2020	-0.084	0.045	-1.90	0.058
	Disturbed unlogged	0.133	0.096	1.39	0.165
	Disturbed extensively logged	**0.326**	**0.094**	**3.46**	**0.0005**
	Disturbed intensively logged	**0.453**	**0.093**	**4.87**	**<0.0001**

Table 2: Coefficient estimates of the generalized linear mixed model with Poisson distribution testing the effect of sampling year (Year), deadwood amount (Deadwood), canopy openness (Canopy openness) and the interaction between deadwood amount and canopy openness on the number of species of aculeate Hymenoptera and saproxylic beetles per plot. Significant parameters are highlighted in bold.

Group	Model parameter	Estimate	Standard error	z value	P value
Non-cavity-nesting Hymenoptera	**Intercept (Year-2019)**	**1.029**	**0.169**	**6.10**	**<0.0001**
	Year-2020	**0.436**	**0.067**	**6.50**	**<0.0001**
	Deadwood	-0.0005	0.002	-0.29	0.771
	Canopy openness	**0.015**	**0.002**	**6.77**	**<0.0001**
	Deadwood:Canopy openness	0.00005	0.001	1.58	0.115
Cavity-nesting Hymenoptera	Intercept (Year-2019)	-0.590	0.341	-1.73	0.083
	Year-2020	**0.416**	**0.133**	**3.13**	**0.002**
	Deadwood	0.0004	0.003	0.12	0.908
	Canopy openness	**0.017**	**0.004**	**4.14**	**<0.0001**
	Deadwood:Canopy openness	0.00005	0.001	0.96	0.338
Saproxylic beetles	**Intercept (Year-2019)**	**2.942**	**0.117**	**25.12**	**<0.0001**
	Year-2020	-0.084	0.045	-1.90	0.058
	Deadwood	0.001	0.001	0.78	0.434
	Canopy openness	**0.0061**	**0.001**	**4.61**	**<0.0001**
	Deadwood:Canopy openness	-0.00003	0.001	-1.19	0.236

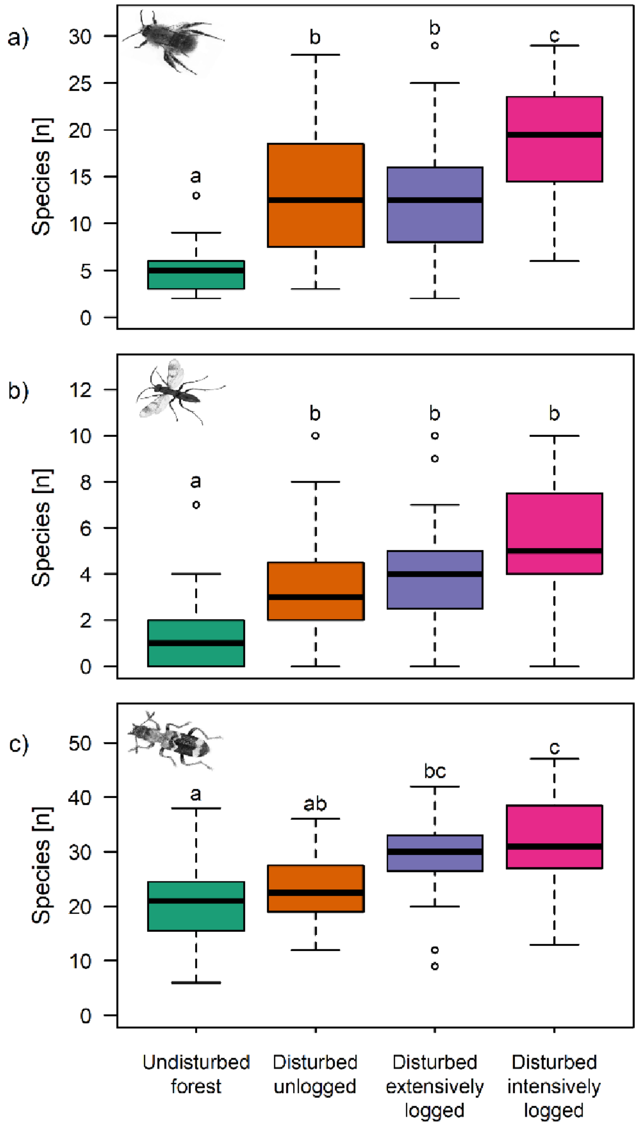

Figure 3: Number of species of a) non-cavity-nesting Hymenoptera, b) cavity-nesting Hymenoptera and c) saproxylic beetle diversity in each treatment. Different letters above boxplots indicate statistically significant differences (P<0.05).

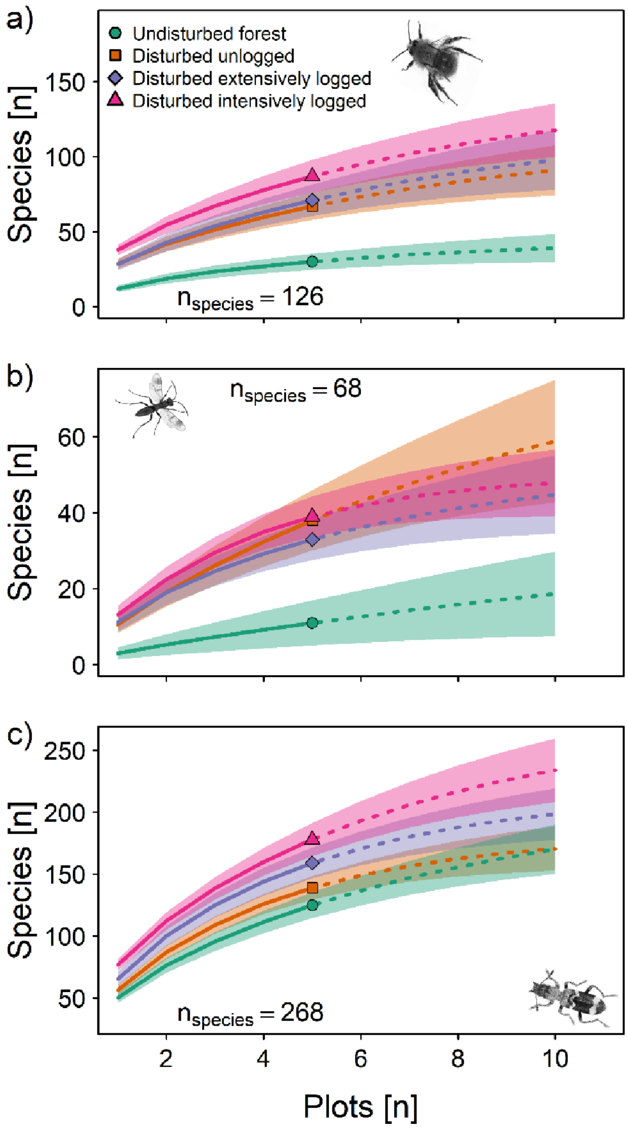

Figure 4: Plot-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the actual sample size) for q=0 of a) non-cavity-nesting Hymenoptera, b) cavity-nesting Hymenoptera and c) saproxylic beetle diversity. Colour shading indicates confidence intervals based on bootstrap replicates. Results for q=1 and q=2 are shown in the Supplementary material (Fig. A.1, Fig. A.2).

Permutational multivariate analysis of variance revealed a significant effect of the treatment on communities of all studied insect groups (Table 3). Communities of cavity-nesting Hymenoptera of undisturbed forest plots differed significantly from all disturbed plots (Supplementary material Table A.5). The sampling year strongly affected community composition of all studied insect groups (Table 3). Permutational multivariate analysis of variance also revealed a significant effect of the canopy openness on communities of all groups whereas the deadwood amount had significant effect only on the community of saproxylic beetles (Table 4).

Communities of undisturbed forest of all studied groups appeared most separated from all others in the NMDS ordination (Fig. 5). The similarity percentage analysis revealed *Apis mellifera*, *Andrena wilkella* and *Bombus lucorum* as the most important non cavity-nesters for driving the differences in communities between any possible pair of two treatments (Supplementary material Table A.6). Differences in communities of cavity-nesters between treatments were mostly caused by rubicolous species like *Hylaeus confusus* and *Hylaeus angustatus* or generalist cavity nesters like *Auplopus carbonarius* (Supplementary material Tab A.7). Bark beetles, such as *Xylosandrus germanus*, *Xyleborinus saxesenii*, and *Taphrorychus bicolor* drove differences in communities of saproxylic beetles between treatments (Supplementary material Tab A.8).

Table 3: Effects of treatment and sampling year on community composition of aculeate Hymenoptera and saproxylic beetles based on permutational analysis of variance with 999 permutations. Significant variables highlighted in bold.

Group	Predictor	Sum of squares	R^2	F value	P value
Non-cavity-nesting Hymenoptera	**Sampling year**	**2.09**	**0.08**	**7.94**	**0.005**
	Treatment	**3.51**	**0.14**	**4.43**	**0.005**
Cavity-nesting Hymenoptera	**Sampling year**	**2.00**	**0.07**	**5.37**	**0.005**
	Treatment	**2.83**	**0.11**	**2.52**	**0.005**
Saproxylic beetles	**Sampling year**	**3.07**	**0.12**	**11.08**	**0.005**
	Treatment	**2.46**	**0.09**	**2.97**	**0.005**

Table 4: Effects of deadwood volume (Deadwood), canopy openness, and sampling year on the community composition of aculeate Hymenoptera and saproxylic beetles based on permutational analysis of variance with 999 permutations. Significant variables highlighted in bold.

Group	Predictor	Sum of squares	R^2	F value	P value
Non-cavity-nesting Hymenoptera	**Sampling year**	**20.95**	**0.08**	**83.40**	**0.005**
	Deadwood	0.31	0.01	12.36	0.31
	Canopy openness	**38.82**	**0.15**	**154.55**	**0.005**
Cavity-nesting Hymenoptera	**Sampling year**	**20.22**	**0.08**	**52.79**	**0.005**
	Deadwood	0.34	0.01	0.88	0.71
	Canopy openness	**15.08**	**0.06**	**39.38**	**0.005**
Saproxylic beetles	**Sampling year**	**30.66**	**0.12**	**114.48**	**0.005**
	Deadwood	**0.40**	**0.02**	**14.81**	**0.035**
	Canopy openness	**24.63**	**0.09**	**91.94**	**0.005**

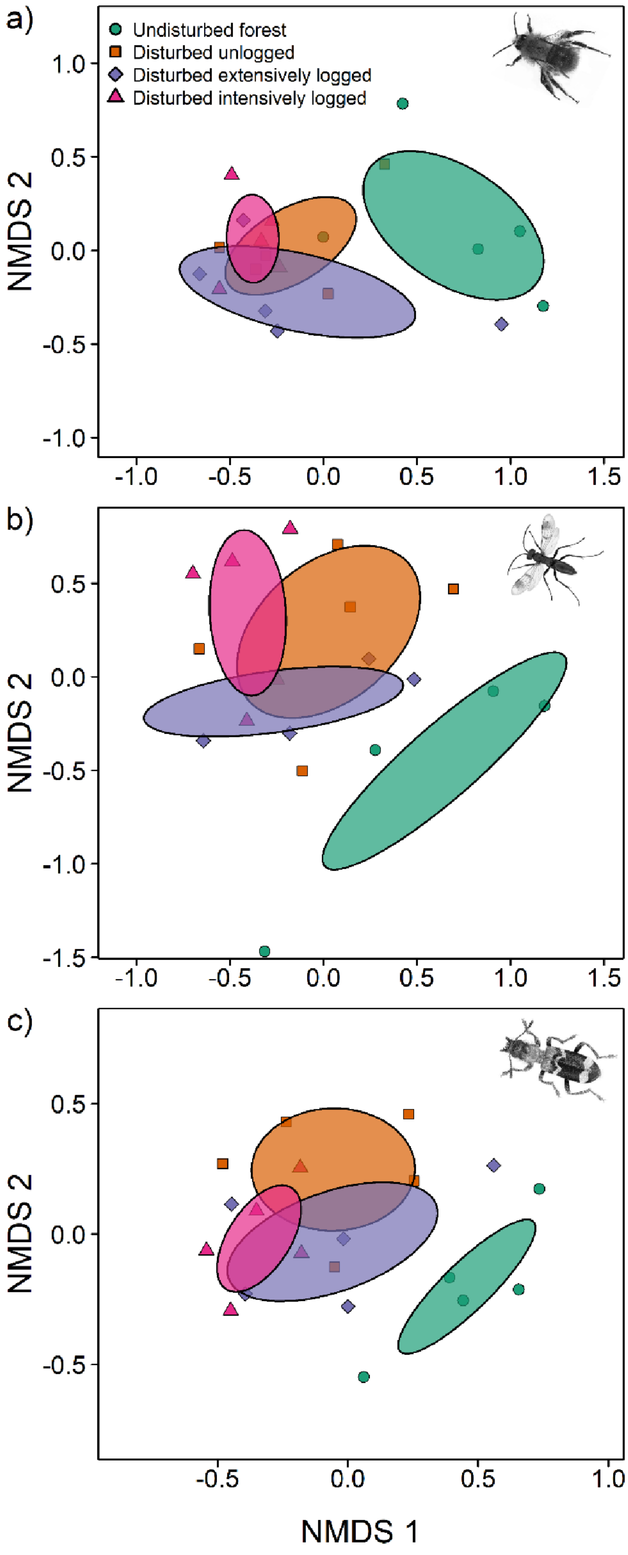

Figure 5: Non-metric multidimensional scaling of a) non-cavity-nesting aculeate Hymenoptera, b) cavity-nesting aculeate Hymenoptera and c) saproxylic beetle communities pooled on the plot level. Ellipses were drawn around the centroids of data points for each treatment and represent 95% confidence space.

4. Discussion

The results of our study confirmed the hypotheses that the increase in canopy openness leads to an increase in the number of species of aculeate Hymenoptera and saproxylic beetles, and that the communities of these groups differed between undisturbed and disturbed forest plots. On the other hand, deadwood amount had only a minor effect on the community composition of saproxylic beetles. All studied insect groups were less species-rich in undisturbed forest. Non-cavity-nesting Hymenoptera and the saproxylic beetles tended to be richest in disturbed intensively logged plots.

4.1. Effect of treatment

In general, the species numbers and community composition of all focal insect groups differed between undisturbed forest and disturbed plots and at the same the undisturbed forest was the poorest among the treatments in terms of alpha and gamma diversity (Fig. 3 and Fig. 4, Table A.5). Differences in the species numbers of Hymenoptera between disturbed treatments and undisturbed forest were evident and more pronounced than in saproxylic beetles, where only disturbed treatments subject to salvage logging were significantly richer. This corroborates the view that disturbances leading to increased canopy openness are essential drivers of insect biodiversity in temperate forests (Martikainen, Bulletins and Debris, 2001; Franc and Götmark, 2008; Müller *et al.*, 2015; Sebek *et al.*, 2015; Wermelinger *et al.*, 2017; Hilmers *et al.*, 2018; Doerfler *et al.*, 2020a; Vymazalová *et al.*, 2021; Weiss *et al.*, 2021). Disturbance primarily affected the diversity of studied insects via increased canopy openness combined with the onset of succession in the logged plots. The logged plots provided open and sunlit ground which promoted increased abundance in flowering plants as a resource for pollen/nectar feeding insects (Bouget and Duelli, 2004; Stevens *et al.*, 2015; Zolotarjova, Kraut and Lõhmus, 2016). In disturbed unlogged plots, on the other hand, the onset of the vegetation succession might have been slowed down because the fallen trees as well as remaining leaf litter may limit the amount of light reaching the ground level.

It is important to note that the treatments within each block were relatively close to each other. Aculeate Hymenoptera are a group with good dispersal capabilities, even small species of aculeate Hymenoptera can forage within several hundred metres from nest with mean foraging distances of tens of metres (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010). So despite the fact that the hymenopterans were likely able to reach all the available treatments in a single block, they clearly avoided the undisturbed forest. While flight-interception trap catches can be affected by insect activity which, in turn, can be affected by openness (and increased temperatures), aculeate Hymenoptera are known to be selective in their foraging habitat and tend to avoid unfavourable habitats (Woodgate *et al.*, 2016; Roberts, King and Milam, 2017). Regarding saproxylic beetles, activity density differs in different habitats with different environmental conditions (Kaspari *et al.*, 2022). The logged plots probably attract saproxylic beetles in a very similar way as the disturbed unlogged ones, there being fresh deadwood available at both. However, as the intensively logged plots offer deadwood of mostly small diameters, beetles may spend more time by actively searching for suitable resources. They may be more prone to detection in intensively logged plots than in disturbed unlogged plots where they find suitable substrates promptly. Nevertheless, species accumulation curves (Fig. 4) can be interpreted as species richness standardized by activity density and allows an unbiased assessment of gamma diversity (see Gotelli and Colwell, 2001 and Chao, Chiu and Jost, 2014).

4.2. Minor effect of deadwood amount

Deadwood amount played only a minor role in our short-term study. Although two of the studied insect groups are directly associated with deadwood, it only had an effect on the community composition of saproxylic beetles (Table 4). Deadwood amount was highest in the disturbed unlogged plots, while the disturbed intensively logged plots had similar deadwood amounts as the undisturbed plots – about 20 m^3/ha in median (Fig. 2a). This is particularly significant, since the local forest enterprise aimed to increase the amounts of deadwood over past decades with positive effects on biodiversity (Roth *et al.*, 2019; Doerfler *et al.*, 2020). We found the lowest species numbers of saproxylic beetles in the undisturbed forests and their numbers increased with increasing openness across the treatments, peaking in the disturbed intensively logged plots (Fig. 3c, Fig. 4c), thus disregarding the amounts of deadwood. Many saproxylic organisms which require early decay stages of deadwood, i.e. recently fallen or still standing trees or tree microhabitats, prefer also high canopy openness (Jonsell *et al.*, 1998; Stokland, Siitonen and Jonsson, 2012; Sebek *et al.*, 2016; Lettenmaier *et al.*, 2022). Forest stands with higher canopy openness have a more diverse microclimate, floral and nesting resources, and sunlit deadwood (Franc and Götmark, 2008; Koch Widerberg *et al.*, 2012; Horák *et al.*, 2018; Lettow *et al.*, 2018). Our results hence indicate that, once the local deadwood amount exceeds a certain level, the absolute amount of deadwood is probably not the most important factor in determining the richness of saproxylic beetles, but it may have an effect on the community composition (Müller and Bütler, 2010; Lachat *et al.*, 2013; Zolotarjova, Kraut and Lõhmus, 2016). It is known that the effect of openness and increased deadwood insolation may outperform the effect of deadwood amount (Müller, Brustel, Brin, Bussler, Bouget, Obermaier, Ina M M Heidinger, *et al.*, 2015). Moreover, insect communities following natural disturbances appear to be predominantly driven by environmental constraints at the start of succession, such as the ease of access to the disturbed plots (Kozel *et al.*, 2021) or the availability of fresh deadwood of a specific tree species, and not by competition for existing deadwood resources, i.e. deadwood amount is generally not a limiting factor (Thorn, Bässler, *et al.*, 2016).

On the other hand, we only studied the communities in the first two years after disturbance and over a longer timeframe the role of deadwood amount may increase significantly. Coarse woody debris, i.e. deadwood of greater diameters, is key to saproxylic beetles on naturally disturbed sites because it supports specialized saproxylic diversity up to several decades after the disturbance event (Schiegg, 2001; Harmon *et al.*, 2004; Müller-Using and Bartsch, 2009; Bouget, Larrieu and Brin, 2014). Also, the most endangered saproxylic beetles are often the largest ones (Seibold *et al.*, 2015; Hagge *et al.*, 2021) and these require large deadwood for development. Development of larger species can also take longer than two years so small-diameter deadwood, which dries out and degrades quickly, usually in two to four years based on microclimate (Harmon *et al.*, 2004; Thorn *et al.*, 2014), does not meet their ecological requirements. It has been confirmed that deadwood diameter affects the species composition of saproxylic beetles (Brin *et al.*, 2011; Bouget *et al.*, 2013). The relative importance of large-diameter deadwood compared to canopy openness may therefore be underestimated in our short-term study and further studies should quantify the effect of variable deadwood amount and its interaction with openness over a longer term.

4.3. Effect of canopy openness

Canopy openness, together with treatment identity, was the most significant predictor determining species numbers in all study groups. Disturbed intensively logged plots had higher canopy openness compared to undisturbed forests while having similar deadwood volumes, underlining the importance of canopy openness compared to deadwood amount in determining hymenopteran communities (Fig 2b). This finding is supported by other studies where openness was the major factor affecting the number of species within woodland habitats (Sutherland, 2002; Benes *et al.*, 2006; Fayt *et al.*, 2006; Sebek *et al.*, 2016; Roberts, King and Milam, 2017). Increased canopy openness in gaps affects insolation and rainfall to the understory and forest floor as well as associated temperature and alternatively humidity (Anderson, Loucks and Swain, 1969; Vickers and Palmer, 2000; Horváth *et al.*, 2023). Both ecological groups of hymenopterans are equally affected by the availability of flowering plants close to their nesting sites (Potts *et al.*, 2005; Grundel *et al.*, 2010; Roberts, King and Milam, 2017) so conditions in gaps that promote vegetation succession and the growth of flowering plants also benefit hymenopterans. Some studies suggest that the number of hymenopteran species in closed, shady forest stands may be similar to open forest environments, but their abundance is only high in spring before leaf-flush, when light-demanding plant species of the forest floor bloom (Bouget and Duelli, 2004; Proctor *et al.*, 2012).

Communities of aculeate Hymenoptera differed significantly between undisturbed forest and all disturbed plots. The differences in composition and species numbers were hence found between the shadiest plots and the rest, and logging intensity was not important. A possible explanation for this finding is that cavity-nesting Hymenoptera might be more affected by e.g. cavity availability, quality and shading of these cavities, and cavity microclimate variability (Potts *et al.*, 2005; Grundel *et al.*, 2010). In contrast to cavity-nesting Hymenoptera, the non-cavity-nesting hymenopterans benefited most from intensive logging. These species most commonly nest in the ground and primarily search for places with sunlit bare ground (Michener, 2007; Budrys, Budriene and Nevronyte, 2010; Grundel *et al.*, 2010; Taki *et al.*, 2013; Bennett, Gensler and Cahill, 2014; Thorn, Bußler, *et al.*, 2016; Campbell *et al.*, 2017). Larger open patches with bare soil created by machinery during intensive salvage logging thus promoted the conditions for this group.

The community composition of saproxylic beetles also differed between undisturbed forest and all other treatments (Fig. 5). This finding is in line with other studies, depicting changes in community composition with increasing canopy openness (Vodka, Konvicka and Cizek, 2009; Seibold *et al.*, 2016; Sebek *et al.*, 2022). Here, similarity percentages revealed that mostly bark beetles, such as e.g. *Xylosandrus germanus*, *Xyleborinus saxesenii*, and *Taphrorychus bicolor,* drove differences in communities of saproxylic beetles between treatments (Tab A.8). These species can colonize deadwood quickly in the early stages of succession. Furthermore, they can influence community composition via changing the occurrence and abundance of predators and commensals (Weslien, 1992).

4.4. Effect of sampling year

We used the sampling year as a covariate in our analyses and found a significant increase of species numbers of Hymenoptera from the first to the second year. We cannot exclude a potential effect of between-year variations in weather conditions (Roberts, King and Milam, 2017; Lindman *et al.*, 2020). However, two years after the initial disturbance, logged plots showed a clear succession onset, with abundant early-successional plants and shrubs (mainly *Rubus* sp. and graminoids). This is also visible in our simper analysis, where cavity-nesting species that had the greatest impact on communities across treatments were species of the genus *Hylaeus*, which frequently nest in grass stems or *Rubus* (Table A.7). Early successional plants tend to be rich in nectar and allow for an influx of nectarivorous species of insects as well as herbivores and their predators, parasites and parasitoids (Rackham, 2008; Proctor *et al.*, 2012; Taki *et al.*, 2013; Roberts, King and Milam, 2017). The effect of sampling year was significant also for community composition of saproxylic beetles, although not for species numbers. Longer-term studies have similarly documented changes in saproxylic beetle assemblages already in the first few years after disturbance (Thorn *et al.*, 2014; Kozel *et al.*, 2021).

5. Conclusions

Our study points out that canopy openness is a major driver of community turnover and increasing species numbers of aculeate Hymenoptera and saproxylic beetles in two years after a disturbance event in the temperate forests. Deadwood amount did not affect the studied insect communities considerably, most likely because the amount of deadwood was high even in intensively salvage-logged plots. Our findings may serve as a baseline for the development of sustainable post-disturbance management strategies, which would aim to increase stand openness while allowing for the removal of a given amount of timber for economic purposes at the same time. However, our findings should be completed by further mid- and long-term studies in order to assess the impact of variable salvage logging intensities on the biodiversity of forest-associated insects following early succession.

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Appendix

Supplementary material

Table A.1: List of collected species and individuals of saproxylic beetles.

Species	**Count**			
	Undisturbed forest	**Disturbed unlogged**	**Disturbed extensively logged**	**Disturbed intensively logged**
Acrulia inflata		1		
Agrilus angustulus		2	3	2
Agrilus biguttatus				3
Agrilus olivicolor		1	2	4
Agrilus sulcicollis			2	3
Agrilus viridis		1	2	1
Allecula morio	1	1	1	1
Alosterna tabacicolor				1
Ampedus balteatus	3	11	19	38
Ampedus brunnicornis				1
Ampedus elongatulus		1	2	1
Ampedus erythrogonus	2	3	5	10
Ampedus nigrinus	3	3	13	27
Ampedus pomorum	7	44	54	76
Ampedus sanguineus			1	13
Ampedus sanguinolentus				1
Amphotis marginata	1			
Anaspis costai				1
Anaspis flava			2	
Anaspis frontalis	1	10	7	3
Anaspis ruficollis	1	3		1
Anaspis rufilabris	8	5	5	2
Anaspis thoracica	3	2	2	
Anidorus nigrinus				1
Anisandrus dispar	98	429	257	353
Anobium punctatum			1	
Anomognathus cuspidatus			1	
Anostirus castaneus		15	12	31
Anostirus purpureus	6	19	9	76
Anthaxia helvetica				1
Anthaxia quadripunctata			5	10
Aplocnemus nigricornis	16	6	6	6
Arhopalus rusticus			1	
Arthrolips obscura				1
Atomaria diluta		2		1
Atomaria ornata	1			
Atomaria pulchra				1
Atomaria turgida	2	1	1	2

Atrecus affinis				1
Attagenus punctatus		1		1
Batrisus formicarius	1			
Bibloporus bicolor	3		1	1
Bibloporus minutus		1		
Bitoma crenata				2
Bolitophagus reticulatus	15	1	6	13
Bostrichus capucinus			2	
Callidium aeneum	2			
Calopus serraticornis	1	1	1	
Cerylon fagi		1		
Cerylon ferrugineum		1	1	
Cerylon histeroides	1	2	1	4
Cetonia aurata		1	1	7
Cis castaneus				1
Cis festivus				1
Cis hispidus	3	1		2
Cis micans				1
Cis quadridens				1
Cis rugulosus		1	1	
Clypastraea pusilla	1			
Clytus arietis		9	5	11
Colydium elongatum				2
Colydium noblecourti		1		1
Conopalpus brevicollis			4	1
Conopalpus testaceus	1			
Corticaria abietorum	2			2
Corticeus linearis			1	
Cortodera femorata				3
Cortodera humeralis		1		
Cryphalus asperatus	5	1	3	1
Cryptophagus dorsalis	16	3	6	7
Crypturgus cinereus	1			
Crypturgus pusillus				1
Crypturgus subcribrosus	1			
Cyclorhipidion bodoanum	12	125	81	115
Cychramus luteus		2	2	1
Dacne bipustulata	1	5	17	19
Dadobia immersa			1	
Dasytes aeratus		3	8	9
Dasytes caeruleus	1	6	8	10
Dasytes niger		3	2	1
Dasytes plumbeus	10	27	19	10
Dasytes virens	1	2		2
Denticollis linearis		1	1	5
Denticollis rubens			1	
Dictyoptera aurora	1			1
Dorcatoma punctulata	1		6	
Dorcatoma robusta			1	2

Drapetes mordelloides			1	2
Dromaeolus barnabita		1	1	
Dryocoetes autographus	3		3	4
Dryocoetes villosus			1	
Dryophilus pusillus		1		1
Endomychus coccineus				1
Enicmus atriceps	8	1		1
Enicmus brevicornis	10	10	7	3
Enicmus fungicola		1	2	1
Enicmus testaceus			1	
Ennearthron cornutum		2	2	3
Epuraea marseuli		1		1
Epuraea neglecta	1			
Ernobius abietinus	1			
Ernobius abietis	1			1
Ernobius mollis		1	1	
Ernobius nigrinus			1	2
Ernoporicus fagi	32	15	19	12
Euglenes oculatus		2		
Euplectus mutator	1	1		
Euryusa castanoptera				1
Euryusa optabilis				2
Gabrius splendidulus			1	
Gastrallus immarginatus				2
Glischrochilus quadripunctatus	1	1	2	1
Hadrobregmus pertinax	1		1	1
Hemicoelus canaliculatus	1			
Hemicoelus costatus	25	5	19	15
Hemicoelus fulvicornis			1	
Holobus apicatus		1		
Homalota plana			2	
Hylastes ater	2			
Hylastes attenuatus	2		2	3
Hylastes brunneus	14	1	3	6
Hylastes cunicularius	8	1	3	2
Hylastes opacus	2		1	
Hylecoetus dermestoides	2	3	2	7
Hylesinus varius	2	3	1	1
Hylis olexai	2		1	1
Hylobius abietis	1		1	1
Hylurgops palliatus	11	2		1
Hyperisus plumbeum	3		4	10
Hypnogyra angularis			1	
Chrysobothris affinis		1	1	1
Ips acuminatus		1		
Ips cembrae		24	3	2
Ips typographus		1	1	
Ischnomera cinerascens			1	1
Ischnomera cyanea	1	1		

Laemophloeus kraussi			1	
Laemophloeus monilis		1		
Latridius hirtus		1		1
Leiopus nebulosus		1		
Leptophloeus alternans				1
Leptura quadrifasciata				1
Leptusa pulchella			1	
Litargus connexus	4	17	19	31
Magdalis cerasi			1	
Magdalis exarata		1		
Magdalis violacea				2
Malachius bipustulatus	1		2	3
Malthinus facialis	2		2	
Malthinus flaveolus	25	18	86	10
Malthodes fuscus	3	1	1	
Malthodes pumilus	1	1		
Malthodes spathifer	3	2	3	1
Megatoma undata	4	6	2	2
Melandrya barbata			1	
Melandrya caraboides		1		2
Melanotus castanipes	15	3	4	1
Melasis buprestoides	5	1	5	1
Microrhagus pygmaeus		1	2	
Molorchus minor	1		1	1
Mordella brachyura		2		
Mordella holomelaena		11	11	24
Mordella huetheri		2	4	8
Mordellistena neuwaldeggiana	1			
Mordellochroa abdominalis	1	1	9	3
Mycetina cruciata		1		
Mycetochara maura	3			
Mycetophagus atomarius	2			1
Mycetophagus quadriguttatus	1			1
Mycetophagus quadripustulatus	1		1	
Nemozoma elongatum	5	2	9	4
Obrium brunneum				1
Octotemnus glabriculus				1
Opilo mollis		1		
Orchesia fasciata			1	
Orchesia undulata			2	1
Orthocis alni				1
Orthoperus atomus	1			
Orthoperus corticalis	11	4	2	3
Pachytodes cerambyciformis		1		4
Paromalus flavicornis	1			
Phloeophagus lignarius	1			
Phloeopora corticalis			2	1
Phloeopora scribae			1	

Phloeostiba lapponica	2			
Phloeotribus spinulosus	1	1		1
Phymatodes testaceus			2	1
Pityogenes bidentatus	1		3	6
Pityogenes chalcographus	24	16	30	29
Pityophthorus lichtensteinii			2	
Pityophthorus pityographus	5	4		4
Placonotus testaceus		2		
Plagionotus arcuatus		2	1	2
Platycerus caraboides	7	10	26	44
Platypus cylindrus			3	2
Platyrhinus resinosus			1	
Platystomos albinus		1	1	2
Plectophloeus fischeri			1	
Plegaderus dissectus	1		1	
Polygraphus poligraphus				1
Prionus coriarius				1
Pseudocistela ceramboides			1	2
Ptenidium gressneri	1			
Ptilinus pectinicornis	6	6	8	6
Ptinomorphus imperialis	18	4	9	10
Pyrochroa coccinea			1	4
Pyrrhidium sanguineum	2	3	6	5
Quedius xanthopus	4	1		
Rhagium inquisitor				3
Rhagium mordax		13	5	19
Rhizophagus bipustulatus	2	2	4	6
Rhizophagus depressus	1			1
Rhizophagus fenestralis				1
Rhizophagus ferrugineus				1
Rhizophagus perforatus		1		1
Rutpela maculata	1	14	9	44
Salpingus planirostris	1	2	1	1
Salpingus ruficollis	1	3	1	1
Scaphidium quadrimaculatum			1	
Scaphisoma agaricinum		2		
Scolytus intricatus	28	28	20	11
Scraptia fuscula		1		
Schizotus pectinicornis		1	2	
Silvanoprus fagi	1			
Silvanus unidentatus	1			
Sphindus dubius				1
Stenagostus rhombeus	1		2	3
Stenopterus rufus		2	1	
Stenurella melanura	4	22	19	45
Stephostethus alternans	7	4	3	3
Stephostethus rugicollis				1
Stictoleptura maculicornis		2	2	6
Stictoleptura rubra	10	4	20	17

Stictoleptura scutellata	1	1		1
Sulcacis affinis		2	2	1
Sulcacis fronticornis		1		1
Symbiotes gibberosus				1
Synchita variegata			2	1
Tachyta nana			1	2
Taphrorychus bicolor	56	266	236	192
Tetropium castaneum	2		1	
Tetropium fuscum	1			
Thanasimus femoralis				1
Thanasimus formicarius	5	3	3	1
Tilloidea unifasciata		1	3	6
Tillus elongatus	1	1	1	4
Tomicus piniperda	3			
Tomoxia bucephala	1	12	14	51
Triplax rufipes	2	10	5	5
Triplax russica		4	1	
Tritoma bipustulata	1	1	3	1
Tropideres albirostris		1	1	
Trypodendron domesticum	9	4	1	
Trypodendron lineatum	5			1
Trypodendron signatum	25	21	38	15
Uleiota planatus			1	2
Uloma culinaris				1
Valgus hemipterus		24	35	44
Variimorda villosa		1	3	6
Vincenzellus ruficollis	17	4	8	4
Xyleborinus attenuatus	2	2		
Xyleborinus saxesenii	213	798	430	1563
Xyleborus monographus	3	5	7	9
Xyletinus ater	1			
Xylopertha retusa				1
Xylosandrus germanus	805	124	185	157
Xylostiba monilicornis			1	
Xylotrechus antilope		6	2	2

Table A.2: List of collected species and individuals of non-cavity-nesting Hymenoptera and their nest parasites.

Species	**Count**			
	Undisturbed forest	**Disturbed unlogged**	**Disturbed extensively logged**	**Disturbed intensively logged**
Ammophila sabulosa		2	1	
Andrena agilissima		1		
Andrena barbilabris		1		
Andrena bicolor			2	3
Andrena bimaculata		1		

Andrena cineraria	4	28	30	53
Andrena confinis	1	1	1	1
Andrena dorsata		5	4	7
Andrena flavipes	2	17	20	49
Andrena fucata	4	18	8	24
Andrena fulva	3	8	5	6
Andrena fulvata			1	
Andrena gravida	2	3	2	5
Andrena haemorrhoa	20	18	23	27
Andrena helvola		1	1	1
Andrena jacobi	1		2	2
Andrena labialis			1	2
Andrena lathyri	1		1	1
Andrena minutula	3	12	7	14
Andrena minutuloides		1		
Andrena mitis			2	
Andrena nigroaenea		4	13	14
Andrena ovatula		9	15	35
Andrena praecox				2
Andrena proxima	1	3	3	3
Andrena vaga				4
Andrena varians	2		1	2
Andrena wilkella	8	57	105	158
Anoplius infuscatus				1
Apis mellifera	31	354	216	274
Arachnospila spissa		1		
Argogorytes mystaceus			1	
Bombus barbutellus				1
Bombus bohemicus	3	16	8	23
Bombus hortorum	3			12
Bombus humilis			1	1
Bombus lapidarius	1	9	17	42
Bombus lucorum	11	53	70	155
Bombus pascuorum	4	21	28	68
Bombus pratorum	3	4	1	3
Bombus rupestris	1			6
Bombus soroeensis				1
Bombus sylvestris	1			2
Bombus terrestris	2	13	24	78
Bombus vestalis		1		6
Colletes cunicularius		3	2	2
Colletes daviesanus		1	1	1
Crabro cribrarius		2		1
Crossocerus varus	2			
Dasypoda hirtipes			1	1
Diodontus luperus			1	
Diodontus minutus			1	1
Diodontus tristis			2	2
Dolichovespula media				1

Epeolus variegatus				1
Eucera nigrescens		1		
Eumenes coronatus		2	1	2
Halictus eurygnathus			1	
Halictus rubicundus		1		1
Halictus scabiosae		4	1	8
Halictus sexcinctus			1	
Halictus simplex		1		
Halictus subauratus		1	1	2
Hedychridium coriaceum			1	1
Hylaeus variegatus		1		
Lasioglossum calceatum		2	2	1
Lasioglossum costulatum		1	3	3
Lasioglossum fratellum			1	
Lasioglossum fulvicorne				1
Lasioglossum lativentre	2	11	5	11
Lasioglossum leucopus			1	
Lasioglossum leucozonium		3	1	
Lasioglossum marginatum				1
Lasioglossum minutissimum				1
Lasioglossum morio		1	1	2
Lasioglossum politum				1
Lasioglossum punctatissimum		1		
Lasioglossum pygmaeum			2	1
Lasioglossum quadrinotatum	1	1		2
Lasioglossum rufitarse		22	11	30
Lasioglossum zonulum				1
Lindenius pygmaeus armatus		1	1	
Macropis europaea				1
Megachile maritima				1
Melitta leporina				1
Mellinus arvensis		1	1	
Nomada concolor		1		1
Nomada fabriciana		1		
Nomada ferruginata				1
Nomada flavoguttata				1
Nomada fulvicornis				2
Nomada goodeniana		1		
Nomada lathburiana		1		
Nomada panzeri			1	
Nomada ruficornis	1			
Nomada signata		1		
Nomada succincta		2	2	
Nomada zonata		1		
Oxybelus bipunctatus			1	1
Oxybelus trispinosus				1
Oxybelus uniglumis			1	1
Oxybelus variegatus		1		
Panurgus calcaratus		1		1

Podalonia affinis		1		
Polistes dominulus		1	1	6
Priocnemis enslini				1
Priocnemis hyalinata		1	1	1
Priocnemis perturbator				1
Priocnemis pusilla	1	3		3
Sceliphron curvatum				1
Sphecodes ephippius			1	
Sphecodes geoffrellus		2	2	2
Sphecodes gibbus				1
Sphecodes hyalinatus			1	
Sphecodes longulus			2	
Sphecodes marginatus		1		1
Sphecodes niger				1
Sphecodes puncticeps			2	
Sphecodes reticulatus			1	
Sphecodes rubicundus	1	14	10	20
Stelis signata		1		
Tachysphex pompiliformis			1	
Vespa crabro		5	1	2
Vespula germanica			2	1
Vespula rufa				1
Vespula vulgaris	5	18	42	14

Table A.3: List of collected species and individuals of cavity-nesting Hymenoptera and their nest parasites.

Species	**Count**			
	Undisturbed forest	**Disturbed unlogged**	**Disturbed extensively logged**	**Disturbed intensively logged**
Agenioideus cinctellus		2		2
Allodynerus rossii		3	4	8
Ancistrocerus claripennis		1		
Ancistrocerus nigricornis	4	2	3	5
Ancistrocerus parietinus		1	1	
Ancistrocerus parietum	1	1		
Auplopus albifrons		1		
Auplopus carbonarius	8	6	5	
Bombus hypnorum			1	3
Crossocerus vagabundus		1		
Deuteragenia bifasciata	1	3	4	
Deuteragenia subintermedia		1		
Deuteragenia variegata			2	
Dolichovespula adulterina	1	1		3
Dolichovespula saxonica	1			2
Dolichovespula sylvestris		1	1	1
Dolichurus corniculus				1

Ectemnius cephalotes	1		1	1
Ectemnius confinis				1
Ectemnius continuus		2		2
Ectemnius lapidarius				1
Ectemnius lituratus			2	1
Ectemnius spinipes		1		2
Heriades crenulatus		1		2
Heriades truncorum				5
Hylaeus angustatus	1	1	1	10
Hylaeus annulatus	1	2	2	8
Hylaeus brevicornis				2
Hylaeus communis		1	2	2
Hylaeus confusus		11	11	40
Hylaeus difformis		2		
Hylaeus gibbus		3		2
Hylaeus hyalinatus			1	
Hylaeus leptocephalus			1	
Hylaeus lineolatus				1
Hylaeus punctatus		1	4	2
Hylaeus signatus			1	
Hylaeus styriacus		1	1	
Chelostoma campanularum			1	
Chelostoma distinctum			1	
Chelostoma foveolatum				1
Chrysis angustula			3	2
Chrysis fulgida			1	
Chrysis impressa		1	1	
Chrysis schencki				1
Chrysis solida		1		1
Chrysis terminata	1	4	2	5
Chrysis viridula		1		1
Megachile centuncularis		1		2
Megachile lapponica				1
Mimumesa dahlbomi			1	
Omalus aeneus			1	1
Osmia bicornis		6	3	5
Osmia cerinthidis				1
Osmia leaina			1	
Osmia uncinata	1			
Pemphredon inornata			1	
Pemphredon lethifera		1		
Pemphredon lugubris		1		
Pemphredon rugifera		1		
Pseudomalus violaceus		1		
Sapygina decemguttata				2
Symmorphus crassicornis			1	1
Symmorphus debiliatus		1	1	5
Symmorphus murarius	1			
Trichrysis cyanea		4	4	

Trypoxylon fronticorne	1	
Trypoxylon minus	2	2

Table A.4: The pairwise comparisons between species numbers of all four treatments. Significant comparisons are highlighted in bold.

Group	Predictor	Estimate	Standard error	z value	P value
Non-cavity-nesting Hymenoptera	Disturbed extensively logged - Disturbed unlogged	-0.09	0.18	-0.46	0.643
	Disturbed intensively logged - Disturbed unlogged	**0.46**	**0.18**	**2.57**	**0.010**
	Undisturbed forest - Disturbed unlogged	**-1.12**	**0.21**	**-5.43**	**<0.001**
	Disturbed intensively logged - Disturbed extensively logged	**0.54**	**0.18**	**3.01**	**0.003**
	Undisturbed forest - Disturbed extensively logged	**-1.03**	**0.21**	**-4.99**	**<0.001**
	Undisturbed forest - Disturbed intensively logged	**-1.57**	**0.20**	**-7.81**	**<0.001**
Cavity-nesting Hymenoptera	Disturbed extensively logged - Disturbed unlogged	0.00	0.33	-0.02	0.988
	Disturbed intensively logged - Disturbed unlogged	0.45	0.32	1.42	0.155
	Undisturbed forest - Disturbed unlogged	**-1.32**	**0.39**	**-3.37**	**0.001**
	Disturbed intensively logged - Disturbed extensively logged	0.46	0.32	1.44	0.151
	Undisturbed forest - Disturbed extensively logged	**-1.32**	**0.39**	**-3.36**	**0.001**
	Undisturbed forest - Disturbed intensively logged	**-1.77**	**0.39**	**-4.58**	**<0.001**
Saproxylic beetles	**Disturbed extensively logged - Disturbed unlogged**	**0.19**	**0.09**	**2.08**	**0.037**
	Disturbed intensively logged - Disturbed unlogged	0.32	0.09	3.51	**<0.001**
	Undisturbed forest - Disturbed unlogged	-0.13	0.10	-1.39	0.166
	Disturbed intensively logged - Disturbed extensively logged	0.13	0.09	1.43	0.153
	Undisturbed forest - Disturbed extensively logged	**-0.33**	**0.09**	**-3.46**	**0.001**
	Undisturbed forest - Disturbed intensively logged	**-0.45**	**0.09**	**-4.87**	**<0.001**

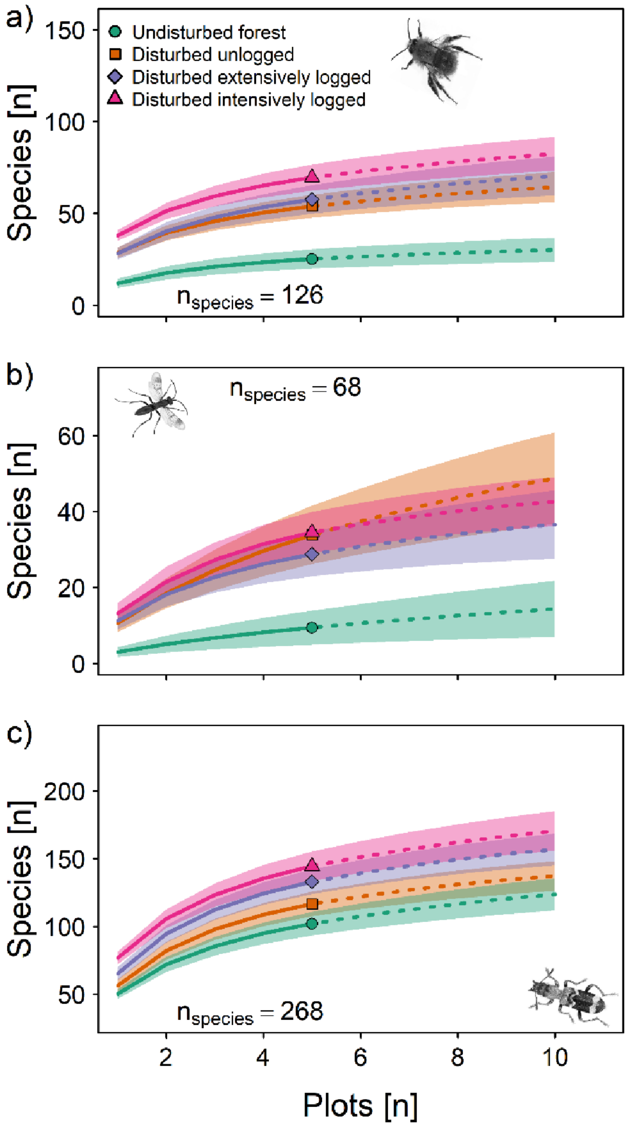

Figure A.1: Plot-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the actual sample size) of a) non-cavity-nesting Hymenoptera, b) cavity-nesting Hymenoptera and c) saproxylic beetles for Shannon diversity ($q = 1$). Colour shading indicate confidence intervals based on bootstrap replicates.

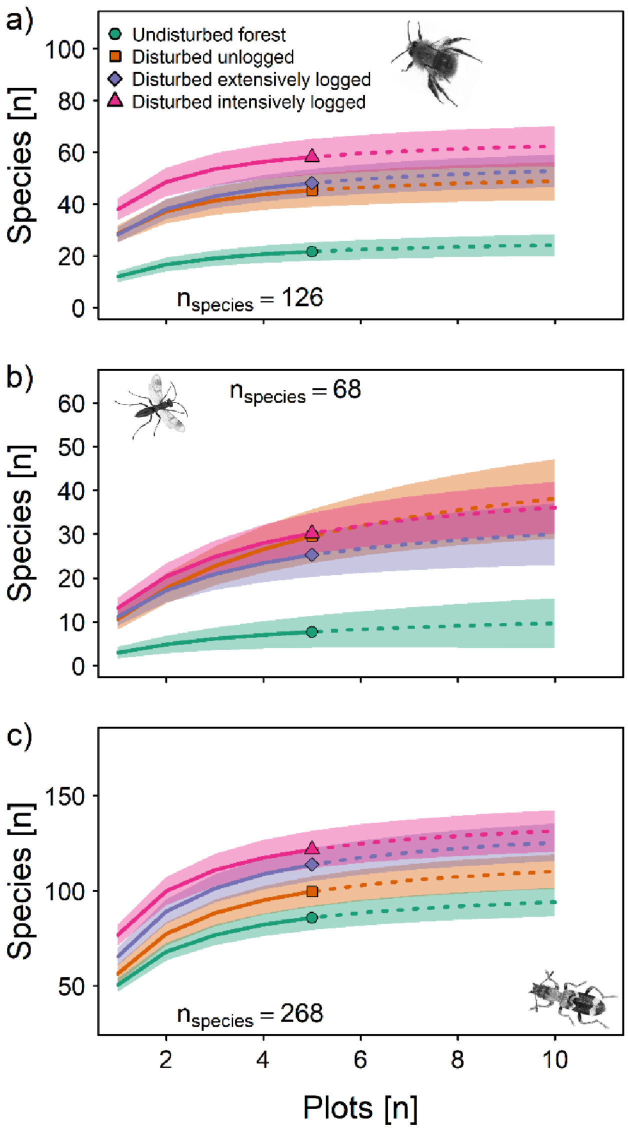

Figure A.2: Plot-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the actual sample size) for Simpson diversity (q = 2) of a) non-cavity-nesting Hymenoptera, b) cavity-nesting Hymenoptera and c) saproxylic beetles. Colour shading indicate confidence intervals based on bootstrap replicates.

Table A.5: Pairwise comparisons of communities in four treatments based on permutational analysis of variance with 999 permutations. Significant comparisons are highlighted in bold.

Group	Predictor	Sum of squares	R^2	F value	P value
Non-cavity-nesting Hymenoptera	**Undisturbed forest - Disturbed unlogged**	**1.33**	**0.10**	**4.42**	**0.03**
	Disturbed extensively logged - Disturbed unlogged	0.46	0.04	1.66	0.09
	Disturbed intensively logged - Disturbed extensively logged	**0.55**	**0.05**	**2.50**	**0.03**
	Undisturbed forest - Disturbed intensively logged	**2.63**	**0.20**	**10.38**	**0.03**
	Disturbed intensively logged - Disturbed unlogged	**0.76**	**0.08**	**3.58**	**0.03**
	Undisturbed forest - Disturbed extensively logged	**1.29**	**0.09**	**4.13**	**0.03**
Cavity-nesting Hymenoptera	**Undisturbed forest - Disturbed unlogged**	**1.04**	**0.09**	**2.72**	**0.03**
	Disturbed extensively logged - Disturbed unlogged	0.35	0.02	0.92	2.88
	Disturbed intensively logged - Disturbed extensively logged	0.81	0.06	2.22	0.06
	Undisturbed forest - Disturbed intensively logged	**1.79**	**0.15**	**5.12**	**0.03**
	Disturbed intensively logged - Disturbed unlogged	0.63	0.04	1.68	0.24
	Undisturbed forest - Disturbed extensively logged	**1.31**	**0.12**	**3.55**	**0.03**
Saproxylic beeltes	**Undisturbed forest - Disturbed unlogged**	**1.08**	**0.08**	**3.84**	**0.03**
	Disturbed extensively logged - Disturbed unlogged	0.30	0.02	1.08	1.20
	Disturbed intensively logged - Disturbed extensively logged	0.47	0.04	1.72	0.30
	Undisturbed forest - Disturbed intensively logged	**1.75**	**0.13**	**6.40**	**0.03**
	Disturbed intensively logged - Disturbed unlogged	0.52	0.04	1.92	0.12
	Undisturbed forest - Disturbed extensively logged	**0.82**	**0.07**	**2.95**	**0.03**

Table A.6: The list of three species of non-cavity-nesting Hymenoptera with the highest impact on the dissimilarity between each two treatment types based on the Bray-Curtis dissimilarities calculated via simper analysis.

Species	Average between group dissimilarity	Standard deviation of contribution	Average to sd ratio	Average abundance in first group	Average abundance in second group	Cumulative contribution
Apis mellifera	0.212	0.195	1.089	17.70	1.55	0.249
Andrena wilkella	0.072	0.097	0.737	2.85	0.40	0.333
Bombus lucorum	0.071	0.071	1.008	2.65	0.55	0.417
Apis mellifera	0.187	0.199	0.943	17.70	10.80	0.243
Andrena wilkella	0.099	0.107	0.929	2.85	5.25	0.373
Bombus lucorum	0.062	0.065	0.957	2.65	3.50	0.453
Apis mellifera	0.151	0.124	1.222	10.80	13.70	0.211
Andrena wilkella	0.088	0.093	0.941	5.25	7.90	0.333
Bombus lucorum	0.076	0.071	1.071	3.50	7.75	0.439
Apis mellifera	0.187	0.113	1.662	13.70	1.55	0.213
Andrena wilkella	0.126	0.122	1.030	7.90	0.40	0.355
Bombus lucorum	0.089	0.086	1.036	7.75	0.55	0.456
Apis mellifera	0.150	0.152	0.984	17.70	13.70	0.209
Andrena wilkella	0.090	0.096	0.939	2.85	7.90	0.335
Bombus lucorum	0.072	0.069	1.052	2.65	7.75	0.435
Apis mellifera	0.164	0.182	0.901	10.80	1.55	0.191
Andrena wilkella	0.147	0.149	0.983	5.25	0.40	0.361
Bombus lucorum	0.077	0.087	0.881	3.50	0.55	0.450

Compared treatments	Average abundance in first group	Average abundance in second group	Cumulative contribution
Disturbed unlogged - Undisturbed forest	0.33	0.80	0.192
Disturbed unlogged - Undisturbed forest	0.61	0.00	0.295
Disturbed unlogged - Undisturbed forest	0.11	0.40	0.368
Disturbed unlogged - Disturbed extensively logged	0.61	0.65	0.123
Disturbed unlogged - Disturbed extensively logged	0.33	0.29	0.199
Disturbed unlogged - Disturbed extensively logged	0.33	0.18	0.263
Disturbed extensively logged - Disturbed intensively logged	0.65	2.11	0.185
Disturbed extensively logged - Disturbed intensively logged	0.06	0.53	0.251
Disturbed extensively logged - Disturbed intensively logged	0.24	0.42	0.300
Disturbed intensively logged - Undisturbed forest	2.11	0.00	0.181
Disturbed intensively logged - Undisturbed forest	0.00	0.80	0.301
Disturbed intensively logged - Undisturbed forest	0.53	0.10	0.381
Disturbed unlogged - Disturbed intensively logged	0.61	2.11	0.184
Disturbed unlogged - Disturbed intensively logged	0.06	0.53	0.254
Disturbed unlogged - Disturbed intensively logged	0.33	0.26	0.308
Disturbed extensively logged - Undisturbed forest	0.29	0.80	0.179
Disturbed extensively logged - Undisturbed forest	0.65	0.00	0.294
Disturbed extensively logged - Undisturbed forest	0.18	0.40	0.368

Table A.7: The list of three species of cavity-nesting Hymenoptera with the highest impact on the dissimilarity between each two treatment types based on the Bray-Curtis dissimilarities calculated via simper analysis.

Compared treatments	**Species**	**Average between group dissimilarity**	**Standard deviation of contribution**	**Average to sd ratio**
Disturbed unlogged - Undisturbed forest	Auplopus carbonarius	0.176	0.196	0.897
Disturbed unlogged - Undisturbed forest	Hylaeus confusus	0.095	0.133	0.712
Disturbed unlogged - Undisturbed forest	Ancistrocerus nigricornis	0.067	0.113	0.597
Disturbed unlogged - Disturbed extensively logged	Hylaeus confusus	0.110	0.124	0.893
Disturbed unlogged - Disturbed extensively logged	Auplopus carbonarius	0.068	0.106	0.638
Disturbed unlogged - Disturbed extensively logged	Osmia bicornis	0.058	0.095	0.606
Disturbed extensively logged - Disturbed intensively logged	Hylaeus confusus	0.168	0.178	0.945
Disturbed extensively logged - Disturbed intensively logged	Hylaeus angustatus	0.061	0.115	0.526
Disturbed extensively logged - Disturbed intensively logged	Allodynerus rossii	0.044	0.072	0.607
Disturbed intensively logged - Undisturbed forest	Hylaeus confusus	0.176	0.222	0.795
Disturbed intensively logged - Undisturbed forest	Auplopus carbonarius	0.116	0.149	0.783
Disturbed intensively logged - Undisturbed forest	Hylaeus angustatus	0.078	0.144	0.546
Disturbed unlogged - Disturbed intensively logged	Hylaeus confusus	0.168	0.184	0.914
Disturbed unlogged - Disturbed intensively logged	Hylaeus angustatus	0.064	0.123	0.520
Disturbed unlogged - Disturbed intensively logged	Osmia bicornis	0.050	0.089	0.559
Disturbed extensively logged - Undisturbed forest	Auplopus carbonarius	0.166	0.170	0.979
Disturbed extensively logged - Undisturbed forest	Hylaeus confusus	0.107	0.148	0.724
Disturbed extensively logged - Undisturbed forest	Ancistrocerus nigricornis	0.069	0.101	0.682

Table A.8: The list of three species of saproxylic beetles with the highest impact on the dissimilarity between each two treatment types based on the Bray-Curtis dissimilarities calculated via simper analysis.

Species	Average between group dissimilarity	Standard deviation of contribution	Average to sd ratio	Average abundance in first group	Average abundance in second group	Cumulative contribution
Xylosandrus germanus	0.158	0.183	0.864	6.20	40.25	0.189
Xyleborinus saxesenii	0.130	0.145	0.897	39.90	10.65	0.344
Taphrorychus bicolor	0.073	0.102	0.713	13.30	2.80	0.431
Xyleborinus saxesenii	0.141	0.164	0.860	39.90	21.50	0.180
Taphrorychus bicolor	0.094	0.111	0.850	13.30	11.80	0.300
Anisandrus dispar	0.083	0.086	0.968	21.45	12.85	0.406
Xyleborinus saxesenii	0.167	0.213	0.787	21.50	78.15	0.213
Taphrorychus bicolor	0.071	0.087	0.821	11.80	9.60	0.304
Anisandrus dispar	0.063	0.071	0.880	12.85	17.65	0.384
Xyleborinus saxesenii	0.154	0.206	0.750	78.15	10.65	0.178
Xylosandrus germanus	0.145	0.175	0.826	7.85	40.25	0.345
Taphrorychus bicolor	0.052	0.056	0.930	9.60	2.80	0.404
Xyleborinus saxesenii	0.187	0.224	0.837	39.90	78.15	0.234
Taphrorychus bicolor	0.076	0.089	0.862	13.30	9.60	0.329
Anisandrus dispar	0.072	0.074	0.970	21.45	17.65	0.419
Xylosandrus germanus	0.160	0.172	0.926	9.25	40.25	0.198
Xyleborinus saxesenii	0.099	0.114	0.871	21.50	10.65	0.321
Taphrorychus bicolor	0.072	0.105	0.685	11.80	2.80	0.410

Compared treatments
Disturbed unlogged - Undisturbed forest
Disturbed unlogged - Undisturbed forest
Disturbed unlogged - Undisturbed forest
Disturbed unlogged - Disturbed extensively logged
Disturbed unlogged - Disturbed extensively logged
Disturbed unlogged - Disturbed extensively logged
Disturbed extensively logged - Disturbed intensively logged
Disturbed extensively logged - Disturbed intensively logged
Disturbed extensively logged - Disturbed intensively logged
Disturbed intensively logged - Undisturbed forest
Disturbed intensively logged - Undisturbed forest
Disturbed intensively logged - Undisturbed forest
Disturbed unlogged - Disturbed intensively logged
Disturbed unlogged - Disturbed intensively logged
Disturbed unlogged - Disturbed intensively logged
Disturbed extensively logged - Undisturbed forest
Disturbed extensively logged - Undisturbed forest
Disturbed extensively logged - Undisturbed forest

Chapter IV

Microbiotope selection in saproxylic bees and wasps (Hymenoptera, Aculeata) – Cavity-nesting communities in forests and wooded pastures are affected by variation in openness but not deadwood

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Chapter IV

Microbiotope selection in saproxylic bees and wasps (Hymenoptera, Aculeata) – Cavity-nesting communities in forests and wooded pastures are affected by variation in openness but not deadwood

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ABSTRACT

Background: Saproxylic insects are an important component of forest biodiversity; however, their ecological requirements are mostly studied on beetles, while other groups are less considered. Aculeate Hymenoptera provide valuable ecosystem services, and some rely on deadwood cavities. We studied cavity-nesting aculeate Hymenoptera using wooden trap-nests set in a heterogeneous partially rewilded woodland area in Central Bohemia, Czech Republic, and tested their nesting preferences in association with canopy openness, amount of deadwood, and the diversity of surrounding vegetation types.

Methods: We used 100 trap-nests in five microbiotopes – forest edge, shady closed-canopy forest, open patches in closed-canopy forest, open-grown trees in wooded pasture, and shady groves in wooded pasture, over two years.

Results: We reared 824 specimens belonging to 26 species of saproxylic hymenopterans. We found no effect of microbiotope on total species richness and richness of nest parasites, but richness of nest builders was highest in forest edge and lowest in open-grown trees in wooded pasture. Species composition of hymenopterans was driven by a wider habitat context: despite the proximity of the habitats, the forest, especially closed-canopy patches, hosted a different community, dominated by wasps, than open wooded pasture. Moreover, open patches in forest differed in composition from the closed-canopy patches, suggesting that in production forests, the diversity of saproxylic hymenopterans may be limited by the overall low share of open canopy stages. Deadwood (amount and diversity) did not affect the saproxylic bees and wasps in any way.

Implications for insect conservation: Our results support conservation measures leading to diversification of the forest canopy and vegetation structure in order to support rich communities of saproxylic Hymenoptera, especially in protected areas.

INTRODUCTION

Saproxylic insects depend on dead or dying woody material at some stage of their life cycle (Speight, 1989; Calix *et al.*, 2010), and they account for approximately one third of all forest insect species (Stokland, Siitonen and Jonsson, 2012; Ulyshen and Šobotník, 2018). They depend on deadwood either directly, by consuming woody parts, bark, and phloem; or indirectly, i.e., they feed on other saproxylic organisms (wood-rotting fungi or other saproxylic invertebrates) or they require deadwood for nesting. Saproxylic organisms contribute to decomposition as secondary wood decomposers and they thus help facilitate the process of nutrient recycling in woodland ecosystems.

Members of several insect orders are saproxylic, the three most diverse of which are beetles (Coleoptera), flies (Diptera), and bees and wasps (Hymenoptera). Moreover, saproxylic species can be found in other insect groups, such as snakeflies (Raphidioptera), true bugs (Heteroptera), and moths (Lepidoptera). Beetles are considered to be the most diverse group of saproxylic insects. Around 25% of all beetle species in Europe are obligatorily or facultatively saproxylic (Bouget, Larrieu and Brin, 2014; Seibold *et al.*, 2015). While the numbers of saproxylic species of Diptera and Hymenoptera have yet to be quantified, their species richness might well be as high, or even higher, than that of beetles (Stokland, Siitonen and Jonsson, 2012). Nevertheless, beetles, due to their well-known taxonomy and relatively easy identification, are by far the most studied group of saproxylic insects. Conclusions about the relationships between habitat characteristics and the biology or diversity of saproxylic insects are therefore mostly based on beetles (Bouget, Larrieu and Brin, 2014; Horak *et al.*, 2014; Müller *et al.*, 2015; Miklín *et al.*, 2017; Gimmel and Ferro, 2018; Hilmers *et al.*, 2018), while other insect groups are less represented in the literature (Fayt *et al.*, 2006; Ricarte *et al.*, 2007; Quinto *et al.*, 2012; Ramírez-Hernández *et al.*, 2014; Hilszczański, 2018). This could lead to potential problems in biodiversity assessments of forest habitats and in conservation management policy if the patterns in saproxylic beetle diversity are not comparable with the requirements of other saproxylic groups (Müller *et al.*, 2020).

Saproxylic Hymenoptera are represented mostly by the parasitoid families Braconidae and Ichneumonidae, the wood-boring sawfly families Xiphydriidae and Siricidae, wood dwelling ants (Formicidae), and secondary cavity dwelling aculeate families (Chrysididae, Vespidae, Pompilidae, Sapygidae, Crabronidae, Megachilidae, Apidae, and others). Aculeate Hymenoptera are among the most effective pollinators, and their habitat requirements and biodiversity have been well studied, especially in the context of open habitats and anthropogenic landscape changes (Ulrich, 1999; Quintero, Morales and Aizen, 2010; Williams *et al.*, 2010; Heneberg, Bogusch and Řezáč, 2017). Pollinators have been facing the same, if not greater, biodiversity loss as other insect groups, mostly due to agricultural intensification, traditional management abandonment, and habitat loss (Biesmeijer *et al.*, 2006; Grundel *et al.*, 2010; Quintero, Morales and Aizen, 2010; Schüepp *et al.*, 2011; Vanbergen *et al.*, 2013; Roberts, King and Milam, 2017). Aculeate Hymenoptera also include many species of predators (wasps) and parasitic species which fulfil valuable ecosystem services like pest control (Picanço *et al.*, 2011; Ebeling *et al.*, 2012; Prezoto *et al.*, 2019; Brock, Cini and Sumner, 2021).

Despite growing recognition that forests provide important habitats for saproxylic bees and wasps (Bogusch and Horák, 2018; Falk, 2021) and that the group is sensitive to management decisions (Westrich, 1996; Westerfelt *et al.*, 2015; Hanula, Ulyshen and Horn, 2016; Lettow *et al.*, 2018), few specific guidelines have been developed for supporting their diversity in forests (Potts *et al.*, 2010; Bogusch and Horák, 2018). At the same time, saproxylic bees and wasps differ from saproxylic beetles in their biology and ecology. Development time in saproxylic beetles takes about two years on average (with smaller species developing in one year, but very large species up to four or five years), whereas aculeate Hymenoptera have short generation time: the development from egg to adult usually takes no longer than one year, with some species having several generations per year. Therefore, aculeate Hymenoptera diversity and abundance reflects ongoing real-time habitat development. Hymenoptera also predominantly feed on nectar as adults, some require it for offspring (bees), and therefore their diversity depends on the existence of feeding patches which must be found within optimal foraging distance from their nesting site (Westrich, 1996; Gathmann and Tscharntke, 2002; Greenleaf *et al.*, 2007; Grundel *et al.*, 2010; Bennett, Gensler and Cahill, 2014). The nesting site, however, does not need to be rich in such resources, and many species are able to nest in shady habitats (Potts *et al.*, 2005; Fabian *et al.*, 2013; Taki *et al.*, 2013). For instance, about 20% of European species of aculeate Hymenoptera nest in various cavities, beetle galleries, hollow branches, or naturally occurring cavities in deadwood. Such wood cavities can be expected to occur where most deadwood occurs, i.e., in forests, rather than outside them in open habitats. Therefore, although in general deadwood-dependent cavity-nesting Hymenoptera may prefer open habitats with available food resources for foraging, they may, in contrast, predominantly search for nesting sites in shady environments under the tree canopy due to higher incidence of deadwood substrates there or due to specific microclimate conditions.

Untargeted sampling methods may also add to the lack of clarity about requirements of saproxylic Hymenoptera in this context. The most commonly-used coloured pan traps sample foraging individuals and may be effective in sampling only part of the species pool (Leong and Thorp, 1999; Heneberg and Bogusch, 2014) or those affected by local flower availability (Heneberg and Bogusch, 2014; Acharya *et al.*, 2021; Westerberg *et al.*, 2021). Alternatively used passive window-flight interception traps (Sebek *et al.*, 2016, Perlík *et al.*, 2023) can catch individuals that are only passing through the habitat but not using it for nesting. Even studies focusing on cavity-nesting bees and wasps rarely target saproxylic species specifically. Instead, they focus on all cavity-nesting species, thus including also the majority of those that utilise other substrates than wood for nesting, e.g. stems of herbs, straw, etc. (Tscharntke, Gathmann and Steffan-Dewenter, 1998; Tylianakis *et al.*, 2006; Bogusch and Horák, 2018). Moreover, studies on cavity-nesting Hymenoptera are often carried out either in forest habitats only or in anthropogenic environments such as orchards, fields, or gardens (Gathmann, Greiler and Tscharntke, 1994; Tylianakis, Klein and Tscharntke, 2005; Roberts, King and Milam, 2017) where the effect of distance to forest or forest edge on communities is explored.

In the present study, we focus on cavity-nesting bees and wasps utilising deadwood as a nesting substrate, using wooden trap-nests as a sampling method. We compare species numbers, community composition and parasitism rates of saproxylic aculeate Hymenoptera in a forest environment with different levels of canopy openness as well as in adjoining woody pastures with diverse open and shady patches. We also assess the importance of other environmental predictors such as the amount of deadwood or diversity in the vegetation structure surrounding nests of cavity-nesting bees and wasps in order to examine basic patterns in the requirements of this group.

MATERIAL AND METHODS

Study site and sampling design

The study was carried out in the former military training area of Milovice, Central Bohemia, Czech Republic (Fig. 1), in the Traviny grazing reserve and forests surrounding it (50.2836N, 14.8761E). In the past, the area used to be frequently disturbed by heavy army vehicles until its abandonment in 1989. Succession then took place for 26 years until 2015, when a natural grazing (trophic rewilding) conservation management was introduced including herds of wild horses (Exmoor ponies) and European bison (*Bison bonasus*) to the area. The Traviny grazing reserve is now 260 ha of wooded pastures with a heterogeneous habitat mosaic from taxonomically and structurally varied grasslands and bare soil, with scattered woody plants (predominantly hawthorn *Crataegus* sp., poplar *Populus* sp., and birch *Betula pendula*), to shady groves of closed canopy *Crataegus-Prunus* dominated shrubs. It is surrounded by open land, i.e., crop fields and a golf course, but also by a forest to the north and south, predominantly composed of mixed-species stands dominated by oak (*Quercus petraea*) and an admixture of other trees, e.g. pine (*Pinus sylvestris*), birch (*Betula* sp.), *Populus* spp., *Prunus avium*, etc.

We used wooden trap-nests to sample cavity-nesting aculeate Hymenoptera in the wooded pasture and the adjoining forest. The trap-nests were composed of nine wooden blocks (3x3x10 cm each) with one drilled cavity in each block (Fig. 1). The drilled cavities were of three different diameters (6, 8, and 10 mm); each trap-nest thus contained three blocks of each diameter. We selected these diameters based on prior knowledge of the local fauna and their preferred nesting cavity sizes, in order to create nesting opportunities for most of the locally present species. The trap-nests were attached to tree or shrub trunks at approximately 1.5 m above ground with cavity openings facing southeast. The trap-nests were installed in the wooded pasture as well as in the adjoining forest, but in microbiotopes with different levels of canopy openness. These microbiotopes were: (i) south-facing forest edge (i.e. the border between the wooded pasture and forest), (ii) shady forest (places inside the forest with high canopy cover, hereinafter as ‘forest–shady’), (iii), open gaps in forest (gaps of different sizes with low canopy cover, hereinafter as ‘forest–open’), (iv) solitary trees in pasture (‘pasture–open’), and (v) shady groves in pasture (places inside the pasture with high canopy cover of trees, hereinafter as ‘pasture–shady’) (Fig. 1a). Therefore, we sampled both open and shady environments in two contrasting habitats and within a short flying distance, accessible for all local species of aculeate Hymenoptera. Twenty trap-nests were installed in each microbiotope, thus altogether 100 trap-nests, but with half the traps installed in 2018, and the other half in 2019.

Trap-nests were installed from 11 May – 9 September in 2018 and from 4 May – 14 September in 2019 and checked biweekly for occupancy. Occupied blocks were taken for rearing and replaced with empty blocks of the same cavity diameter. This was done to keep the same number of nesting opportunities throughout the whole sampling period (hence to keep the attractiveness of the trap the same) so that even species that are active in the middle of the season or later could find a place to nest. The rearing took place in the laboratory at room temperature until November; each block was covered with mesh immediately after collection and emerging adults were taken for identification. Some species of aculeate Hymenoptera overwinter before emerging, therefore, during the winter months (December and January), blocks were deposited in a climate box at 0 °C and 60% humidity. After overwintering, the rearing continued until the emergence rate of adults dropped to almost nil, then the trap-nests were all opened, and all developed specimens were also collected for identification as their inability to emerge could have been caused by handling of the block during fieldwork or in the laboratory rather than by insufficient conditions of their original microbiotope. All emerged specimens of aculeate Hymenoptera were identified to species level where possible according to the available literature (Schmid-Egger, 2002; Amiet *et al.*, 2004; Paukkunen *et al.*, 2015). The voucher specimens were stored in the depository of the Institute of Entomology, Biology Centre CAS (IECA; Evenhuis, 2023). All species records were uploaded to NDOP (species occurrence database) of the Nature Conservation Agency of the Czech Republic.

For each trap-nest, we recorded several environmental variables describing the immediate surroundings of the trap, such as openness, amount of deadwood in 2 and 10 m around the trap, the amount of standing or downed deadwood, the number of trees around the trap, or the mean diameter of the trees around the trap (Table 1), and we also calculated several variables describing the amount of habitat types and their diversity at 50 and 150 m around the traps using Geographic Information Systems (GIS) (Fig. 1b). The area of the study site was classified into land-cover categories based on aerial photographs from the years of study (2018, 2019). All land-cover estimations were performed with ArcGIS Pro software (ESRI, 2011). The pixel resolution of aerial photographs across the study site was resampled to 1 m^2. The forest land-cover categories were created by means of manual vectorization based on a previous field survey. Land-cover categories in forest were: plantations, mixed closed forest, open forest, semi-open forest, and clearing. The vegetation cover of the wooded pasture was classified by unsupervised K-means pixel-based clustering (Hamfelt *et al.*, 2011). Based on K-means classification and following field interpretation, the main land-cover categories were: closed bushes, scattered bushes, tall grassland, short grassland, sparse grass, and bare ground. See Table 1 for more details about the recorded environmental variables.

In 2019, we installed one microclimate datalogger in each of the five studied microbiotopes in order to illustrate potential differences in temperature, humidity, and dew point. The loggers were placed next to the traps (Fig. 1d) and were set to record data every hour during the entire sampling period (for microclimate data overview see Table S1).

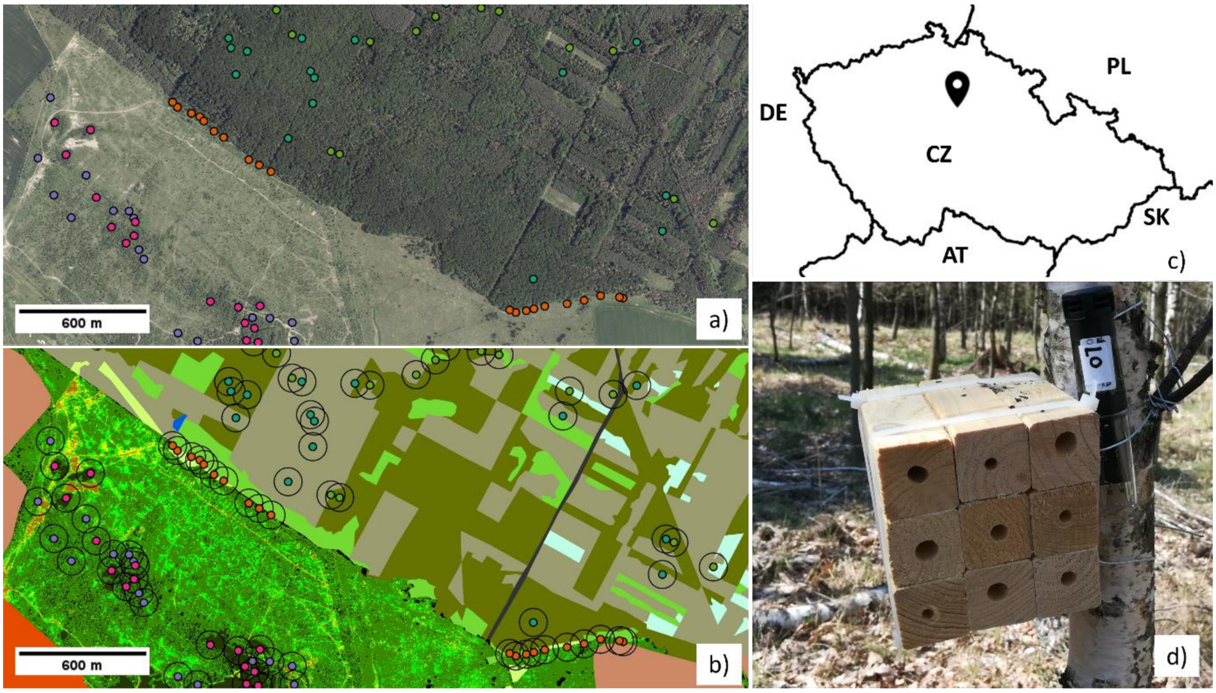

Fig. 1 Trap-nests and their distribution. Visualisation of the positions of traps (different colours for different microbiotopes) at the study site (a): brown dots = forest edge, light green = open gaps in forest (forest-open), dark green = shady forest, (forest-shady), violet dots = shady groves in pasture (pasture-shady), pink dots = solitary trees in pasture (pasture-open). The GIS land cover layer (b) shows different colours for different types of marked habitats, i.e., mature plantation forest, mixed forest, closed bush, clearings, tall grassland, short grassland, and bare ground; the circles around the traps represent the 50 m buffers around the traps. A simplified map of the Czech Republic with the study site location is also given (c). The cavity-nesting bees and wasps were collected using trap-nests composed of nine blocks with one drilled hole in each block (hole diameters of 6, 8, 10 mm) (d); one datalogger was installed in each microbiotope type in 2019 to record microclimatic conditions (the black datalogger is placed next to the trap).

Table 1 List of recorded environmental variables with their descriptions, units, and observed range.

Name of variable	Description	Units	Range
Openness	Percentage of open sky in 10m around the trap, measured visually (0 = fully shaded, 100 = fully open-grown)	%	10-90
Permeability	Degree to which a space in front of the trap is overgrown/obstructed by branches and leaves (visually in a 1m^3 cube in front of the trap (100 = fully obstructed, 0 = fully open)	%	5-65
Trees in 2m	Number of trees (tree trunks) in a 2m circle around the trap	count	1-21
Trees in 10m	Number of trees (tree trunks) in a 10m circle around the trap	count	1-90
Mean DBH in 2m	Mean diameter of trees in a 2m circle around the trap (measured at 1.3m above ground)	cm	2-55
Mean DBH in 10m	Mean diameter of trees in a 10m circle around the trap (measured at 1.3m above ground)	cm	3-45
Amount of deadwood in 2m	Amount of deadwood in a 2m circle around the trap (on scale 0-5)	semi-quantitative	0-3
Amount of deadwood in 10m	Amount of deadwood in a 10m circle around the trap (on scale 0-5)	semi-quantitative	0-3
Standing small deadwood in 2m	Amount of standing small diameter (<1cm) deadwood in a 2m circle around the trap	semi-quantitative	0-4
Standing small deadwood in 10m	Amount of standing small diameter (<1cm) deadwood in a 10m circle around the trap	semi-quantitative	0-4
Standing large deadwood in 2m	Amount of standing large diameter (>1cm) deadwood in a 2m circle around the trap	semi-quantitative	0-4
Standing large deadwood in 10m	Amount of standing large diameter (>1cm) deadwood in a 10m circle around the trap	semi-quantitative	0-4
Downed small deadwood in 2m	Amount of downed small diameter (<1cm) deadwood in a 2m circle around the trap	semi-quantitative	0-3
Downed small deadwood in 10m	Amount of downed small diameter (<1cm) deadwood in a 10m circle around the trap.	semi-quantitative	0-4
Downed large deadwood in 2m	Amount of downed large diameter (>1cm) deadwood in a 2m circle around the trap	semi-quantitative	0-4
Downed large deadwood in 10m	Amount of downed large diameter (>1cm) deadwood in a 10m circle around the trap	semi-quantitative	0-4
Forest habitats in 50m	Area of forest land cover habitat types (i.e., monoculture, mixed forest, dense shrubs etc.) in a 50m circle around the trap (mapped using GIS)	m^2	0-7833
Forest habitats in 150m	Area of forest land cover habitat types (i.e., monoculture, mixed forest, dense shrubs etc.) in a 150m circle around the	m^2	0-70625

	trap (mapped as land cover type using GIS)		
Open habitats in 50m	Area of open habitats (i.e., bare ground, short grassland, tall grassland, forest clearings, etc.) in a 50m circle around the trap (mapped using GIS)	m^2	0-7832
Open habitats in 150m	Area of open habitats (i.e., bare ground, short grassland, tall grassland, forest clearings, etc.) in a 150m circle around the trap (mapped using GIS)	m^2	0-69629
Habitat diversity in 50m	Number of different land cover categories in a 50m circle around the trap (mapped using GIS)	count	1-9
Habitat diversity in 150m	Number of different land cover categories in a 150m circle around the trap (mapped using GIS)	count	1-12

Statistical analysis

We tested the effect of microbiotope (forest edge, forest-shady, forest-open, pasture-open, pasture-shady) and the effect of environmental variables on species richness and community composition of aculeate Hymenoptera (bees and wasps) emerging from the trap-nests.

Assuming spatially autocorrelated structure of our data, we fitted generalized linear mixed models with Poisson distribution (*log* link function) using the 'glmmTMB' package (Brooks *et al.*, 2017) in R 4.3.1. (R Core Team, 2023) with covariance structure based on the spatial coordinates of traps. We tested the effect of microbiotope (explanatory factor variable with five levels) on total species richness of aculeate Hymenoptera (as a response variable), and then separately on richness of nesters (i.e., species that actively build their brood cells) and richness of brood cell parasites (hereinafter ‘nest parasites’). Sampling year was added to the model as a covariate. Interaction between the effects of microbiotope and year was also tested to see whether the microbiotopes affected species numbers differently in different years.

Then we performed a forward selection of all other environmental variables (without microbiotope type). We first fitted a null model containing richness of hymenopterans as a response variable, intercept, and sampling year as a covariate and then added sequentially significant variables into the model starting with the variables with the lowest AIC value in comparison to the null model. We performed the forward selection procedure with the whole dataset but then also created two subsets: one containing only trap-nests from the forest (forest-shady, forest-open), and another one containing trap-nests only from the pasture (pasture-shady, pasture-open). We did this because the resolution of land cover variables differed between the two habitats; e.g., the diversity of land cover types was lower for trap-nests in the forest than in the pasture, which might mask the potential effect of it on occupancy by bees and wasps.

We then analysed the parasitism rate in each microbiotope using the ratio between the number of emerged individuals of nest parasites and all emerged individuals (nest parasites and nesters) from each trap. As nearly all aculeate hymenopteran nest parasites replace one host larva with one larva of their own, each emerged nest parasite also represents one host larva which was removed or devoured by the nest parasite. We used a generalized linear mixed model with binomial distribution (*logit* link function) with parasitism rate in each trap as a response variable, microbiotope as an explanatory variable, and sampling year as a covariate. We added the covariance structure assuming spatial correlation between samples to the model. To evaluate host availability in each microbiotope, we displayed the total number of emerged individuals (abundance of all bees and wasps) in microbiotope types and tested the number of emerged individuals from traps using the generalized linear mixed model with Poisson distribution and spatial covariance structure.

Further, we analysed the effect of microbiotope type on community composition of cavity-nesting Hymenoptera using multivariate ordination methods. We used Principal Coordinates of Neighbouring Matrices (PCNM) to first filter out the effect of space (which was significant in preliminary analysis of community composition) and then to test the clear effect of microbiotope type (used as an explanatory factor variable) with sampling year added as a covariate to the model. We then performed a forward selection of other measured environmental variables without microbiotope added to the model to assess if they affect species composition independently. We used a matrix of species abundances as response variables; the abundances were log-transformed and rare species down-weighted before calculating the models to lower the weight of species occurring in a single sample. Significance of the variables was tested by Monte Carlo tests with 999 permutations. The ordination analyses were carried out and visualised using Canoco 5.15 (Ter Braak and Šmilauer, 2018).

Finally, we performed an indicator species analysis, using the 'indicspecies' package in R (De Cáceres & Legendre, 2009), which estimates the strength of associations of species to levels of a factor variable. With this approach we assessed whether some species are indicative of a particular microbiotope type or combinations of up to three types.

RESULTS

During the two-year sampling of cavity-nesting aculeate Hymenoptera, we reared 26 species (824 individuals) of bees, wasps, and their nest parasites. These included seven bee species (293 individuals), 14 wasp species (including Vespidae, Pompilidae, Sapygidae, and Crabronidae) (464 individuals), and five species of cuckoo wasps (67 individuals). Out of these, 19 species (753 individuals) were true cavity nesters, and seven species (71 individuals) were brood cell parasites (for the list of all species, see Table S2).

The regression analyses showed no effect of microbiotope on total species richness ($\chi^2_{(4)}$=4.92, P=0.296) (Fig. 2a). On average, 1.5 species emerged from a trap. On the other hand, there was a significant effect of microbiotope on the number of nester species ($\chi^2_{(4)}$=11.04, P=0.026), with the lowest numbers of nesters found in pasture-open biotope and the highest at the forest edge (Fig. 2b). The number of nest parasites was highest in pasture-shady biotope and lowest at the edge, but the effect of microbiotope overall was not significant ($\chi^2_{(4)}$=9.05 P=0.059) (Fig. 2c). The interactions between sampling year and microbiotope were not significant, revealing that the effect of microbiotope was independent of year. Only sampling year was thus used as a covariate in the models. The test statistics are given in Table 2; coefficient estimates are displayed in Table S3.

Forward selection testing the effect of other environmental variables on species richness showed no significant association when the whole dataset (100 traps) was used, and also when the subset comprising traps from forest was used. However, when the subset of traps from pasture was used, the analysis revealed a significant positive effect of diversity of habitats in 50 m around the traps ($\chi^2_{(1)}$=5.64, P=0.017); thus the greater the diversity of habitats around traps, the greater the number of species in traps.

The analysis of parasitism rate revealed a significant effect of microbiotope ($\chi^2_{(4)}$=12.31, P=0.015); the pasture-shady biotope had a greater proportion of parasitised brood cells (mean 0.17) than the other microbiotopes (mean 0.06). Parasitism rates are displayed in Fig. 3 along with total abundances (representing brood cell availability); the coefficient estimates of the model are in Table 3. Microbiotope type did not affect abundance of bees and wasps in trap-nests significantly ($\chi^2_{(4)}$=9.06, P=0.059) (Fig. S2).

Principal Coordinates of Neighbouring Matrices (PCNM) revealed significant effect of microbiotope on species composition of cavity-nesting Hymenoptera (pseudo-F=1.6, P=0.006, expl. variation=6.84%) after filtering out the effect of space and the effect of sampling year. The analysis showed that the pasture-open microbiotope differed greatly from the forest habitats and that forest-shady harboured the most distinct composition from other microbiotopes, as it was primarily dominated by three wasp species and one nest parasite associated with wasps. There was also a visible gradient of community change going from forest edge, through forest-open to forest-shady microbiotope. The ordination diagram is displayed in Fig. 4. Other environmental variables did not have any effect after filtering out the effect of space and the effect of sampling year.

Total amount of deadwood and amount of deadwood of diverse types did not affect the richness or community composition of cavity-nesting Hymenoptera, despite that the variation in the variables was high (Fig. S1).

The indicator species analysis revealed that *Osmia bicornis* had high fidelity to forest edge and forest-open microbiotopes; and *Ancistrocerus nigricornis* and *Chrysis terminata*, its nest parasite, had strong association with both pasture microbiotopes (open and shady) (Table S4). Two more species, *Osmia caerulescens* and *Chrysis solida*, were identified by the analysis as highly specific for forest edge and pasture-shady, respectively.

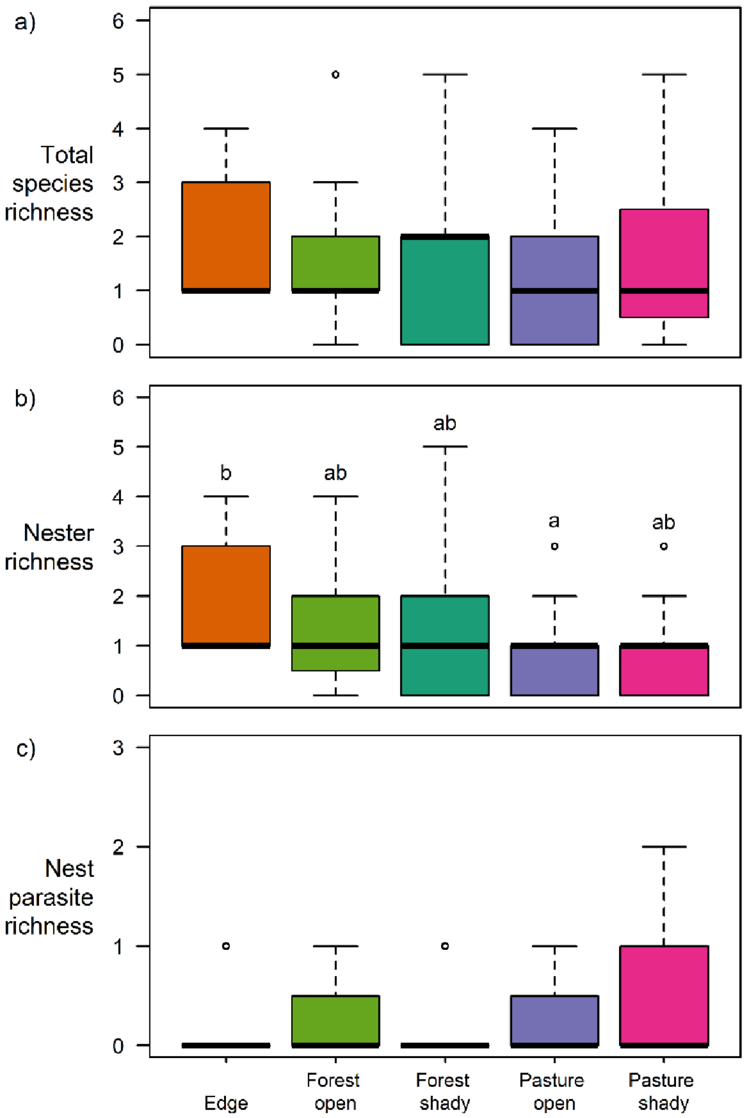

Fig. 2 Boxplots showing a) the total species richness of aculeate Hymenoptera, b) nester species richness, and c) nest parasite species richness in different microbiotopes. The thick lines denote median values; the boxes cover 0.25 to 0.75 percentile of the data. Letters above boxplots indicate statistically significant differences based on Tukey HSD post-hoc comparisons.

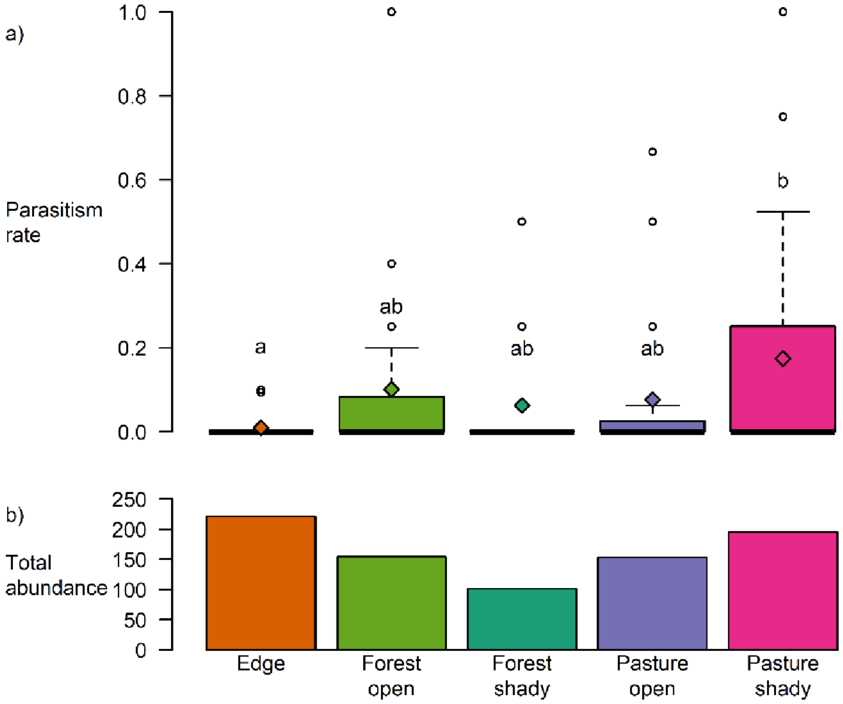

Fig. 3 Observed parasitism rate for all five studied microbiotopes, with mean parasitism rates displayed as coloured diamonds. Letters above boxplots indicate statistically significant differences based on Tukey HSD post-hoc comparisons. The parasitism rate (a) was calculated as a proportion of individuals of nest parasites from all emerging individuals; i.e., abundance of nesters and nest parasites together, and these abundances (b) are displayed for context of the number of possible hosts.

Table 2 Results of the generalised linear mixed models with Poisson distribution testing the effect of microbiotope (edge, forest-open, forest-shady, pasture-open, pasture-shady) and sampling year (covariate) on the number of all cavity-nesting species of aculeate Hymenoptera and on the number of nester species and nest parasite species, separately. Significant effects ($P<0.05$) are marked with an asterisk (*); coefficient estimates of all three models are given in Table SI 3). The interactions between sampling year and microbiotope were not significant in any of the models (all species: $\chi^2_{(4)}=4.51, P=0.34$; nesters: $\chi^2_{(4)}=3.7, P=0.44$; nest parasites: $\chi^2_{(4)}=2.27, P=0.68$).

Group	Predictor	d.f.	χ^2	P value
All species	Microbiotope	4	4.92	0.296
	Year	1	0.09	0.765
Nesters	Microbiotope	4	11.04	0.026*
	Year	1	0.64	0.424
Nest parasites	Microbiotope	4	9.05	0.059
	Year	1	0.57	0.451

Table 3 Coefficient estimates of the generalised linear mixed model with binomial distribution testing the effect of microbiotope (edge, forest-open, forest-shady, pasture-open, pasture-shady) and sampling year on the parasitism rate (proportion of emerged nest parasite individuals to all emerged individuals). Significant tests ($P<0.05$) are marked with an asterisk.

Model parameter	Estimate	Std. Error	z value	P value
Intercept (Edge)	-6.36	1.25	-5.07	<0.001*
Forest-open	2.33	1.19	1.95	0.051
Forest-shady	1.49	1.26	1.18	0.237
Pasture-open	2.55	1.25	2.04	0.041*
Pasture-shady	3.99	1.19	3.36	<0.001*
Year	1.21	0.73	1.66	0.097

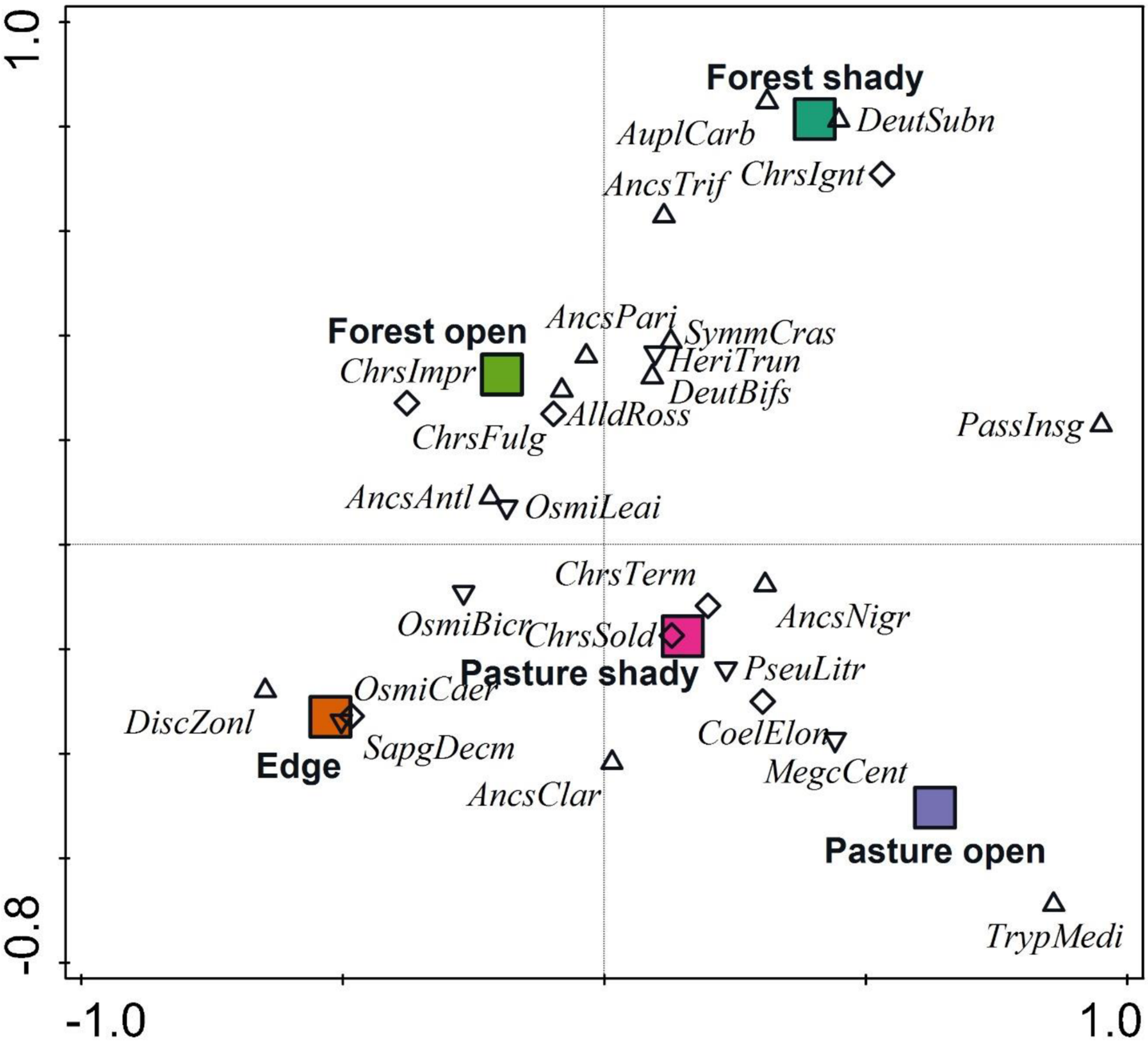

Fig. 4 Ordination diagram of species composition based on the Principal Coordinates of Neighbouring Matrices (PCNM) analysis. The diagram shows the species composition with respect to microbiotope type after filtering out the effects of space and sampling year. The first two canonical axes are displayed: the first axis horizontally, second axis vertically. Symbols for species depend on life histories: triangle = wasp / predatory parasitoid; upside-down triangle = bee / pollen collector; diamond = nest parasite / kleptoparasite. The list of non-abbreviated species names is in the Supplementary information section, Table S2.

DISCUSSION

We investigated saproxylic aculeate Hymenoptera in different habitats of temperate deciduous woodland; and for the first time, we bring information on their nesting preferences in association with canopy openness, amount of deadwood, and other characteristics. We did not find any effect of amount of deadwood or its diversity on the richness and community composition of bees and wasps. Only canopy openness of habitats affected the species composition of the studied assemblages, which corroborates the role of light availability as a major driver of saproxylic insect biodiversity (Fayt et al., 2006; Koch Widerberg et al., 2012; Müller et al. 2015; Thorn et al., 2016). We found that shady habitats in closed-canopy forest hosted a different species composition, dominated by wasps, than habitats in open wooded pasture or forest edge, despite that the microbiotopes were in immediate proximity, and thus within foraging distance of the studied aculeate Hymenoptera. This suggests that the cavity-nesting Hymenoptera are very selective about their nesting sites. It seems that they select the place to nest based on the quality of the nesting site and its immediate surroundings rather than based on the spatial arrangement of the habitats (Morato and Martins, 2006; Grundel *et al.*, 2010), because the habitats with different canopy openness hosted different communities even if they were located close together.

The importance of broader habitat context

Total species numbers and numbers of parasite species did not differ between microbiotopes; the differences were significant only for the number of nester species, but here the difference was relatively small. However, the differences in community composition were relatively substantial, with little overlap between closed-canopy forest, forest edge, and open pasture. Especially the closed-canopy forest biotope hosted communities dominated by wasps, whereas the microbiotopes in pasture, but also at the edge, were predominantly utilised by bees, and a greater share of nest parasites was found there. This suggests that the forest and the pasture, although closely neighbouring, represent distinct habitats and neither serves as a species pool for the other. However, at the same time, the two forest microbiotopes were also relatively distinct, with open patches in forest being closer to the open habitats with their assemblages (Fig. 4), suggesting that heterogeneity in openness may diversify the species assemblages in forests, but in more open habitats the locally measured openness may play a less significant role. The differences between communities of the forest and the pasture were further pronounced by the finding that the number of species in pasture increased with diversity of habitats within a 50 m radius around the trap, whereas richness in forest was unaffected by habitat diversity in their surroundings. This may be associated with structural differences between particular vegetation types. In the pasture, places with short-sward grass, tall grass, or bushes may represent very different structures for bees or wasps, and their richness can be driven by the diversity of these vegetation types, or by variation in the availability of flowers among these vegetation types throughout the season. On the contrary, forests represent a relatively uniform habitat for most of the rotation cycle, so the structural difference between e.g., a 20 year-old stand and a 70 year-old stand may be very small for bees and wasps. Also, flower availability in forests differs from pastures, with the potentially strong effect of spring leaf out and canopy flowering on communities of pollinators and predators in whole forest environments (Urban-Mead *et al.,* 2021, Allen and Davies, 2023).

Our results thus point to the importance of broader habitat context already revealed in other studies (Hoehn, Steffan-Dewenter and Tscharntke, 2010; Schüepp *et al.*, 2011; Rösch *et al.*, 2013). Bees and wasps primarily choose their nesting sites based on a broader scale. They differentiate between the structure of high forests and more open wooded pastures or savanna-like habitats, but after selecting the habitat, the canopy openness of the particular microbiotope within probably plays a less important role for occupation of the nests. The heterogeneity of canopy cover, however, appears to be of some importance to the studied insect group. This can be visible in our ordination diagram (Fig. 4), where homogenous microbiotopes (shady places in forest and open places of open pasture) appear most different, and microbiotopes which include a form of ecotone (open forest patch within shady forest, shady grove within open pasture or forest edge) are most similar in their community composition. Moreover, our collected microclimate data from dataloggers show relatively small differences in temperature, humidity, and dew point among all the five studied microbiotopes (Table S1). Even though both habitats, pasture as well as forest, offer sufficient deadwood nesting opportunities, they differ in availability of other resources like nest building material, host species, pollen and nectar resources, or prey (Dailey and Scott, 2006; de Lima *et al.*, 2020). Previous studies often highlighted the importance of resource-rich patches like flower strips, forest openings, or meadows for Hymenoptera diversity within supposedly poorer habitats like forests or production fields (Kevan, 1999; Krewenka *et al.*, 2011; Fabian *et al.*, 2013; Bennett, Gensler and Cahill, 2014). At the same time, other studies assume benefits of forest cover or its proximity as potential nesting sites to communities of cavity nesters in surrounding open habitats (Tylianakis *et al.*, 2006; Taki *et al.*, 2008; Schüepp *et al.*, 2011; da Rocha-Filho *et al.*, 2017). For instance, Tylianakis (2006) found increasing distance from forest to positively affect the diversity of cavity-nesting bees, but negatively that of cavity-nesting wasps. This is in line with our results, as forest habitat was dominated by wasps, whereas pasture by bees. Different life-histories of the two guilds are responsible for the pattern. Bees are more affected by presence of flower resources, as they must provide their progeny with pollen and nectar (Michener, 2007), making the forest habitat less suitable for nesting, whereas wasps are predatory and provide their larvae with preyed insects and spiders (Morato and Martins, 2006; Brock, Cini and Sumner, 2021). The pattern is, however, not universal in both guilds. In our study, for example, a mason bee *Osmia bicornis* was found to nest in the forest openings and forest edges, potentially because it frequently visits oaks and other trees for pollen collection (Splitt *et al.*, 2021); and conversely, a potter wasp *Ancistrocerus nigricornis* preferred to nest in the pasture (Table S2 and S4).

We studied the nesting requirements of saproxylic bees and wasps, and thus our results offer a possible comparison with saproxylic beetles, the model group traditionally used in deadwood ecology. Communities of saproxylic beetles are largely affected by light conditions, rich assemblages are often concentrated to forest edges, openings, clearings, or open-grown trees outside forests (Bouget, Larrieu and Brin, 2014; Horak *et al.*, 2014; Sebek *et al.*, 2016; Kozel *et al.*, 2021). Sun exposure can be of even greater importance for saproxylic beetles than the amount of deadwood (Müller *et al.*, 2015; Seibold *et al.*, 2016). In production forests, diversity of saproxylic beetles peaks in early-successional stages, on clear-cuts from ca. 0 to 5 years after logging (Hilmers *et al.*, 2018; Kozel *et al.*, 2021). Then the homogeneous, shady structure of mature stands hosts poor assemblages dominated by generalists or mycetophagous beetles (Hilmers *et al.*, 2018). In our study, the shady forest stands were not poorer in number of saproxylic bee and wasp species; they were similarly rich as other habitats, but hosted a different, wasp dominated community.

Lacking association with amount and diversity of deadwood

We did not find any association between deadwood, its amount and quality, and diversity of saproxylic bees and wasps. Deadwood is considered one of the key factors for saproxylic organisms, although its effect may largely be conditioned by sun exposure (Bässler *et al.*, 2010; Müller *et al.*, 2015; Hagge *et al.*, 2019). It seems that the amount of deadwood and its diversity mostly affects saproxylic organisms like fungi and beetles, which use it for their development; i.e., they consume it during development and thus deplete the local deadwood resources over time (Jonsell *et al.*, 1998; Fayt *et al.*, 2006; Ulyshen and Šobotník, 2018). Unlike such saproxylic organisms, cavity-nesting aculeate Hymenoptera only inhabit the deadwood cavities and do not consume deadwood itself; they are rather known to sanitize the cavities to prevent bacterial and fungal contamination of potential brood cells (Michener, 2007). Aculeate Hymenoptera also possess much better flight capabilities in comparison to beetles; they forage effectively in the range of hundreds of metres (Gathmann and Tscharntke, 2002; Greenleaf *et al.*, 2007). This means that cavity-nesting bees and wasps may be virtually unaffected by the total amount of deadwood around their nesting site; the only important factor is the presence of a sufficiently large nest cavity, which can even be present even in small deadwood objects (Budrys, Budriene and Nevronyte, 2010). Taking this into account, cavity nesters can be expected to inhabit a cavity as long as it fulfils their microhabitat requirements; they may select nesting sites based on available nest building materials (type of soil, plant leaves) and food resources within foraging distance from the nest rather than based on the amount of deadwood (Gathmann and Tscharntke, 2002; Potts *et al.*, 2005; Greenleaf *et al.*, 2007), as long as the amount is sufficient (Perlík *et al.*, 2023) (Fig. S1). It would be interesting to test the association between the diversity of cavity-nesting Hymenoptera and the number of naturally occurring holes in the habitats. However, many naturally occurring holes are not easily recognisable, as they may often be cracks or irregularities in wood rather than circular holes. Such an investigation would require a further experimental approach. Also, large solitary trees, i.e. veteran trees, are known to support high saproxylic biodiversity as well as a high number of hymenopteran species (Sebek *et al.*, 2016). In the case of saproxylic organisms, it is likely due to the availability of sunlit deadwood as well as the diversity of available microhabitats, crucial resources for most saproxylic insects (Kraus *et al.*, 2016; Falk, 2021). In the case of bees and wasps, the microhabitat availability likely plays a role together with large trees functioning as landmarks, i.e. navigation points, for foraging flying insects.

Parasitism rate

The highest parasitism rate, on average around 17%, was found in pasture-shady microbiotope, i.e., in the shady bush groves of the pasture; in other microbiotopes, the mean parasitism rate ranged from 1 to 10%, the lowest was found for forest edge. A review suggests that parasitism rate by hymenopteran enemies is generally below 10%, depending on region, onsite diversity of hosts and nest parasites; higher rates are fairly rare, but in some cases, the rate can exceed even 50% (Minckley and Danforth, 2019). The parasitism rate has been found to be driven by richness and abundance of hosts (Staab *et al.*, 2016; Eckerter *et al.*, 2022) or by abundance of food resources (nectar and pollen in the case of bees, arthropod prey in the case of wasps) (Gámez-Virués *et al.*, 2009; Grundel *et al.*, 2010; Jha and Kremen, 2013). In addition, microclimate is known to drive diversity of insects in habitats with different vegetation types or canopy cover (Seibold *et al.*, 2016) and potentially affect the parasitisms (Stangler, Hanson & Steffan-Dewenter, 2015). Dense vegetation (e.g shrubs) may increase microclimate stability required by many insect groups, including hymenopterans, especially their developing stages (Dixon *et al.*, 2009; De Frenne *et al.*, 2021; Wood, Hays and Zinnert, 2020).

In our study, we did not find differences in the total species richness among the microbiotopes, and the abundances of all bees and wasps were similar (Fig. 3, Fig. S2). Therefore, the higher parasitism rate cannot be explained by host diversity or abundance. The significant difference in parasitism rate between forest edge and shady groves in pasture might potentially be explained by resource availability in the broader area around the microbiotope. Higher parasitism rates in sites closer to grasslands (potential resource-rich habitat) were revealed in Tscharntke, Gathmann and Steffan-Dewenter (1998). In our setting, the forest edges were an ecotone of two structurally different habitats, with pasture and forest providing different types of resources, whereas shady groves in pasture were fully surrounded by the heterogeneous pasture. On the other hand, our results are not in agreement with other studies which reported highest parasitism rates at forest edges (Schüepp et al., 2011; da Rocha-Filho et al., 2017) in comparison to forest interior. When only forest habitats were studied, clearings were found to host highest species richness of hosts and associated nest parasites (Eckerter et al., 2022). Such a pattern can be seen in our results, but it was not statistically significant. The above-mentioned studies, however, used reed or bamboo trap-nests and not wooden ones as in our case. It is questionable if microclimate could have affected parasitism rate in combination with food resource availability. The groves in shady pasture had the lowest mean temperature and the lowest maximum temperature (Table S1) out of all microbiotopes, while the open pasture microbiotope had the highest variation in temperatures and humidity, thus potentially hindering development of some species. However, in general, the microclimate differences did not seem great enough; and we cannot reveal this association with our own data, as we used only a single data logger for each microbiotope.

Conclusions

Heterogeneity of woodland biotopes or their successional stages is important for biodiversity of European cavity-nesting bees and wasps. None of the studied microbiotopes hosted considerably higher species richness than the others; however, we show that closed canopy forest habitats were most different in their communities from other more open patches. Patches with open canopies are underrepresented in current production forests as these are usually managed with an 80–120-year rotation cycle. Therefore, such forests do not include late-successional stages, with characteristic large amounts of deadwood and open canopy (Hilmers et al. 2018). The open phases of forest development are therefore mostly limited to clearings (ca. up to 10 years) or small gaps, accounting for only about 10% of the area of forests. This leads to potentially limited capacity for hosting a wide spectrum of saproxylic Hymenoptera. Moreover, the open forest phases are underrepresented even in most protected deciduous and mixed forests in lower and middle elevations of Europe where minimal intervention regimes prevail. In such places, larger scale disturbances occur rarely because their agents (fire, wind, insect outbreaks, large herbivores) have limited effect or have been suppressed on the landscape level. Therefore, forest management measures towards diversifying the canopy of the forest stands (Graser et al. 2023) are indispensable for supporting biodiversity of saproxylic Hymenoptera. At the same time, open habitats with grassy and woody vegetation (shrubs and trees) require measures towards habitat diversification by means of fine scale disturbances, which can be facilitated by temporally diversified grazing, mosaic mowing, heavy vehicle movement, selective burning, etc.

DECLARATIONS

Ethical Approval

All research was done with permission from the landowners of the research sites. No form of ethical approval was required for this study by the legislation of Czech Republic, where the study was undertaken. The research sites were not protected areas and none of the reared insect species were protected by Czech of European laws.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors contributions

MP and PS designed the experiment; MP created the trap-nests; MP and LA performed the field work and recorded environmental data; MP reared and identified the insects from trap-nests; DJ collected the GIS data and analysed it; DJ also created the GIS related figures; MJ provided permits for entry to the research area and assisted in selecting trap sites; MP and PS curated the data; MP and PS analysed the data and wrote the manuscript; PS supervised the study and manuscript writing; All authors contributed to drafts.

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Availability of data and materials

The data that support the findings of this study will be accessible in a public repository (Dryad or Figshare) upon acceptance of the article.

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Supplementary Material

Table S1 Microclimate data measured by data loggers over one vegetation season (2019). Var. coef = variation coefficient, StD = standard deviation.

Microbiotope	Variable	Average	Maximum	Minimum	Var. coef	StD
Edge	Temperature (°C)	18.77	39	-3	0.38	7.09
Forest shady		19.01	41	0	0.33	6.28
Forest open		18.92	42	-1.5	0.37	7.05
Pasture shady		17.87	37.5	-2.5	0.39	7.03
Pasture open		19.09	39	-5	0.42	7.93
Edge	Air humidity (%)	70.71	103.5	21	0.29	20.33
Forest shady		69.4	102	22	0.27	18.54
Forest open		69.58	101.5	21	0.29	20.42
Pasture shady		73.67	101.5	20	0.27	20.05
Pasture open		69.06	101.5	21.5	0.32	21.81
Edge	Dew point (°C)	12.51	23.1	-4.2	0.37	4.61
Forest shady		12.61	22.4	-2.9	0.35	4.45
Forest open		12.39	23.4	-3.4	0.38	4.66
Pasture shady		12.33	24.5	-5	0.37	4.58
Pasture open		12.29	25	-5.5	0.38	4.69

Table S2 List of species of aculeate cavity nesters and their nest parasites reared from trap-nests with their abundances in each microbiotope.

Species	**Abbreviation**	**Edge**	**Forest open**	**Forest shady**	**Pasture open**	**Pasture shady**
Allodynerus rossii	*AllRoss*		4			
Ancistrocerus antilope	*AncAntl*	30	31	16		8
Ancistrocerus claripennis	*AncsClar*	3			1	1
Ancistrocerus nigricornis	*AncsNigr*	2	10	21	105	130
Ancistrocerus parietinus	*AncsPari*	1	2	3		2
Ancistrocerus trifasciatus	*AncsTrif*		2	4		
Auplopus carbonarius	*AuplCarb*			4		
Coelioxys elongata	*CoelElon*				1	
Deuteragenia bifasciata	*DeutBifs*	5	10	19	5	
Deuteragenia subintermedia	*DeutSubn*			3		
Discoelius zonalis	*DiscZonl*	6				
Heriades truncorum	*HeriTrunc*	1		3		1
Chrysis fulgida	*ChrsFulg*		2			
Chrysis ignita	*ChrsIgnt*			2		
Chrysis impressa	*ChrsImpr*		3			8
Chrysis solida	*ChrsSold*					8
Chrysis terminata	*ChrsTerm*	2	4	2	10	26
Megachile centuncularis	*MegcCent*				6	1
Osmia bicornis	*OsmiBicr*	131	77	13	9	3
Osmia caerulescens	*OsmiCaer*	37				
Osmia leaiana	*OsmiLeai*					5
Passaloecus insignis	*PassInsg*			7		
Pseudanthidium lituratum	*PseuLitr*				5	
Sapygina decemguttata	*SapgDecm*	3				
Symmorphus crassicornis	*SymmCras*		9	4		1
Trypoxylon medium	*TrypMedi*				11	1

Table S3 Coefficient estimates of the generalised linear model with Poisson distribution testing the effect of microbiotope (edge, forest-open, forest-shady, pasture-open, pasture-shady) and sampling year and spatial coordinates (covariates) on the number of species of all cavity-nesting Hymenoptera, number of nester species, and number of nest parasite species. Significant tests (P<0.05) are marked with asterisk (*).

Studied group	Variable	Estimate	Std. Error	z(t) value	P value
All species	Intercept (Edge)	0.69	0.19	3.70	<0.001*
	Forest open	-0.26	0.25	-1.03	0.301
	Forest shady	-0.26	0.25	-1.03	0.302
	Pasture open	-0.62	0.28	-2.2	0.028*
	Pasture shady	-0.20	0.25	-0.79	0.428
	Year	-0.05	0.17	-0.3	0.765
Nester species	Intercept (Edge)	0.68	0.17	4.05	<0.001*
	Forest open	-0.39	0.24	-1.65	0.099
	Forest shady	-0.32	0.23	-1.36	0.172
	Pasture open	-0.84	0.28	-3.01	0.003*
	Pasture shady	-0.57	0.25	-2.25	0.025*
	Year	-0.13	0.16	-0.8	0.424
Nest parasite species	Intercept (Edge)	-2.45	0.73	-3.38	<0.001*
	Forest open	0.92	0.82	1.11	0.265
	Forest shady	0.40	0.89	0.45	0.652
	Pasture open	0.92	0.81	1.13	0.260
	Pasture shady	1.7	0.75	2.27	0.023*
	Year	0.28	0.38	0.75	0.451

Table S4 The results of indicator species analysis for best fitting associations of species with microbiotopes. The table shows only significant associations. Specificity is an estimate of the probability that particular species utilises the target microbiotope if it has been reared from a trap in this microbiotope. Fidelity is an estimate of the probability of finding the particular species in traps being set in the microbiotope (or combinations of microbiotopes).

Microbiotope(s)	Species	Specificity	Fidelity	P value
Edge	Osmia caerulescens	1	0.45	0.004**
Pasture shady	Chrysis solida	1	0.39	0.041*
Edge + Forest open	Osmia bicornis	0.89	0.55	0.001***
Pasture open + Pasture shady	Ancistrocerus nigricornis	0.88	0.35	0.34*
	Chrysis terminata	0.82	0.28	0.025*

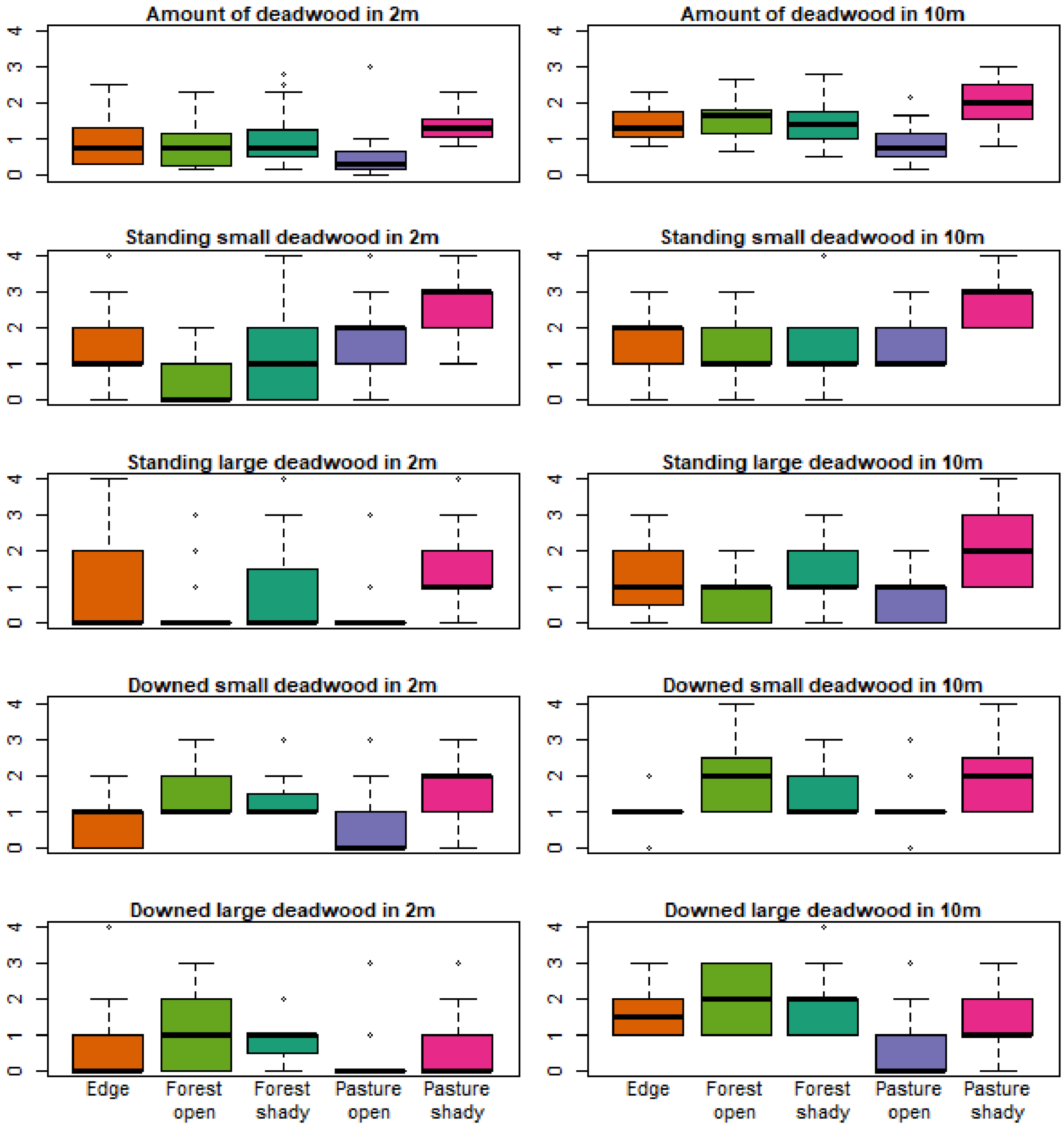

Fig. S1 Amount of various types of deadwood across studied microbiotopes, estimated using a hypothetical scale from 0 to 5. The metres refer to the radius of area surveyed around each trap for particular deadwood type.

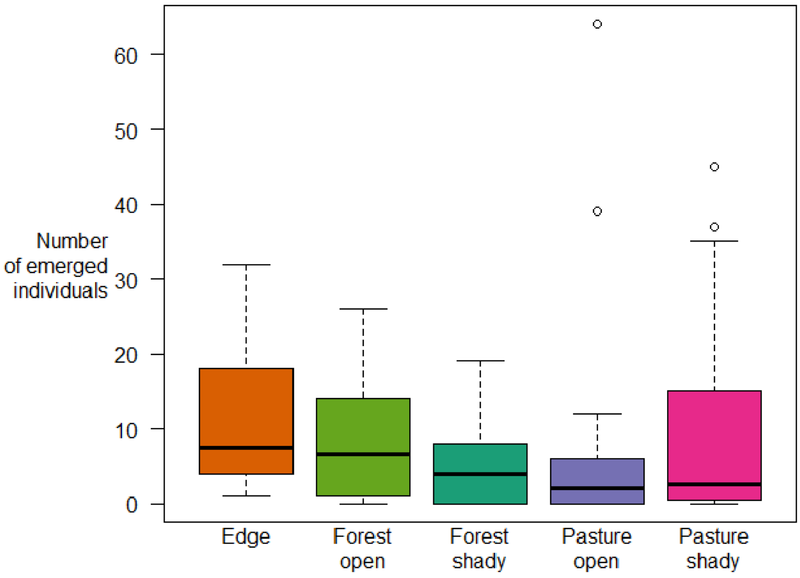

Fig. S2. Number of emerged individuals (abundance) of cavity-nesting bees and wasps from trap-nests installed in five types of microhabitats. The numbers give total abundances of nesters and nest parasites together.

Summary

Summary

In the present thesis, four studies showcase similar patterns in the diversity of woodland aculeate Hymenoptera to those of saproxylic beetles. Most obvious common pattern is the high dependence of species richness on local canopy openness. Also, management practices or disturbance events which promote canopy openness seem to similarly affect both insect groups in our studies.

The studies in this thesis focus mostly on the effects of such management practices or disturbance events while also accounting for other environmental variables which may affect the woodland biodiversity and ecosystem functioning. Testing of the variables revealed very small effect of most variables besides openness or previous management/disturbance on aculeate Hymenoptera. These results suggest habitat selection or site colonization processes by woodland bees and wasps, which may be determined by complex set of variables and their interactions. If such complex environmental characters indeed affect the species richness and overall diversity of woodland bees and wasps, it can easily be overlooked in most studies or masked by other overlaying patterns. Alternatively, microhabitat/microclimate and their fluctuations during the day as well as during the season could be the main habitat selection conditions. Such variables and their effects on diversity can, however, be hard to record in context of an entire habitat. Concurrently, the recording of microhabitat availability is typically time consuming with considerable observer bias. So, while the outcomes of the studies included in this thesis, show similar responses of saproxylic beetles and woodland aculeate Hymenoptera, the reasoning behind these results cannot be conclusively attributed to the same variables in the two insect groups. The deadwood microhabitats and their diversity, tree species diversity and microclimate are crucial for saproxylic beetles. Aculeate Hymenoptera, on the other hand, depend on broader habitat composition, where nesting habitats with sufficient microhabitats and microclimate, and foraging habitats with diverse flower resources and/or prey, are both present within optimal

foraging distances. Both focal insect groups respond to increase in canopy openness of their habitats, with more open early successional or disturbed ones hosting richer communities due to different microclimate from undisturbed mature forest and different microhabitat availability. Interestingly, beyond some minimal thresholds, deadwood amount does not seem to considerably affect neither saproxylic beetles nor cavity nesting aculeate bees and wasps, clearly showing stronger effect of much finer habitat metric, such as the abovementioned microhabitat diversity or microclimate. The used sampling method can also affect the recorded diversity as well as its possible interpretations. The use of flight-intercept traps in three out of the four presented studies, highlights the usefulness of this trapping method not just for beetles, but for the very active aculeate Hymenoptera as well. This also shows that studies focusing on other insect groups and using flight-intercept traps collect a lot of useful data, even though it is often treated as bycatch.

The conservation of woodland invertebrate biodiversity has long been associated with saproxylic taxa such as saproxylic beetles, which are not only vital for the ecological functioning and nutrient cycling of the woodland environments but also suffer from habitat alteration and commercial management. While saproxylic taxa in woodland environments have been well studied in the past, communities of woodland pollinators are often viewed as not so important in conservation. Of course, pollinators are considered an ecologically important insect group. They are, however, typically targeted in open and resource rich environments and not in woodlands and forests. The presented studies showcase the importance of woodland environments and processes affecting them for pollinators (bees) as well as useful predators and pest controlling insects (wasps). While resource rich habitats like steppes, gardens and meadows can host high diversity of foraging pollinators, woodland environments are also vital habitats for this insect group as they can be used for nesting, to buffer climatic extremes or as alternative foraging habitat when the neighbouring open one becomes, for any reason, unsuitable. Woodland environments also tend to have shifted vegetation dynamic compared to the more open ones, allowing flower dependent insects to prolong their foraging on given resource after it is no longer viable in open environments. Tree canopies limit sunlight reaching the forest floor in in peak season, and therefore modify mean temperatures and humidity. This, in turn, delays start of the vegetation season for some plant species, prolonging its end compared to more open habitat. Woodlands with heterogeneous canopy cover over large areas, show variation in such phenology shift creating continuous, prolonged offer of flowering resources like nectar, pollen and other plant material, compared to homogeneous open habitats. Furthermore, woodland environments include wood and deadwood items, which can be used for shelter, nest building or prey collecting. Diversity of such items can further increase the attached diversity. Here, nature conservation efforts can benefit from including pollinators, especially hymenopteran ones, even when planning for forest biodiversity measures. Measures, which positively affect deadwood dependent biodiversity can also add to the diversity of pollinators, and with addition of pollinator-oriented measures such as support of local flowering plants and the diversity of woody vegetation, woodland environments can support species rich assemblages of bees, wasps and other pollinators and predators.

This thesis shows some similarity between the ecological functioning of saproxylic beetles and woodland Hymenoptera but lacks the ability to reveal all the reasons behind those similarities, especially for Hymenoptera. In this way, the specific microhabitat conditions which need to be met for woodland Hymenoptera to thrive in their environment, are likely overshadowed by coarser macrohabitat metrics. For hymenopterans, such microhabitats typically include nesting sites like bare soil patches or deadwood cavities and their respective microclimates, orientations or material. Studies focused on such environmental variables, their variability or availability, are difficult and time consuming to perform and often yield very little convincing results. The difference in flight capabilities between beetles and hymenopterans could also affect the way these two insect groups utilize the environment. The ability of bees and wasp do discover new patches of suitable habitat can greatly differ between habitat types i.e. forest (as well as other habitats with migration barriers such as urban or rocky with deep valleys) is likely more difficult to navigate than in open meadow. While the maximal foraging distances of many bees and wasps are known, they vary considerably between studies and localities, suggesting different habitat permeability based likely on its overall structure. Here, use of mark-recapture or radio tracking approaches can shed some light on flight patterns between different habitats at various distances. Common problem with such approach applied to aculeate Hymenoptera is the diminutive size of many common species as well as the stinging behaviour off females, which can complicate handling and reliable marking of individuals or attachment of tracking devices. Furthermore, use of trap-nests seems to be a valuable additional tool in research of woodland insects as it allows researchers to easily observe nesting behaviour rather than activity (as is the case with flight-intercept traps). In foreseeable future, studies on woodland taxa which use flight-intercept traps, should consider aculeate Hymenoptera as informative part of sampled biodiversity. Such data often already exist but have never been processed and analysed. Hence, their addition to research should be a focus for scientists in the area of forest ecology and conservation. Also, use of structural environmental data measured by like terrestrial laser scan, can add to the interpretative power of forest ecology studies on flying insects as such tools allow to record fine environmental structures on much larger scale and in much shorter time than individual recording. Future research into pollinating insects should include woodland environments, fine structure recording tools, broad landscape landcover/land use information and potentially, use of trap-nests, in combination with flight intercept trap as well as traditional pollinator sampling methods such as coloured pan traps. Woodlands as potential habitats for pollinators should not be omitted from research, and pollinators, like bees and wasps, should not be omitted from woodland conservation efforts and forest ecology research. Hence, the combined research aiming at woodland saproxylic taxa as well as Hymenoptera should be undertaken in order to make well informed conservation decisions that help woodland associated biodiversity.

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Scientific publications with impact factor (IF):

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