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Determinants of saproxylic biodiversity and conclusions for conservation

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Summary

Determinants of saproxylic biodiversity and conclusions for conservation

Over the past centuries, anthropogenic utilization has fundamentally changed the appearance of European forest ecosystems. Constantly growing and changing demands have led to an enormous decline in ecological key elements and a structural homogenization of most forests. These changes have been accompanied by widespread declines of many forest-dwelling and especially saproxylic, i.e. species depending on deadwood. In order to counteract this development, various conservation strategies have been developed, but they primarily focus on a quantitative deadwood enrichment. However, the diversity of saproxylic species is furthermore driven by a variety of abiotic and biotic determinants as well as interactions between organisms. A detailed understanding of these processes has so far been largely lacking. The aim of the present thesis was therefore to improve the existing ecological knowledge of determinants influencing saproxylic species and species communities in order to provide the basis for evidence-based and adapted conservation measures.

In chapter II of this thesis, I first investigated the impact of sun exposure, tree species, and their combination on saproxylic beetles, wood-inhabiting fungi, and spiders. Therefore, logs and branches of six tree species were set up under different sun exposures in an experimental approach. The impact of sun exposure and tree species strongly differed among single saproxylic taxa as well as diameters of deadwood. All investigated taxa were affected by sun exposure, whereby sun exposure resulted in a higher alpha-diversity of taxa recorded in logs and a lower alpha-diversity of saproxylic beetles reared from branches compared to shading by canopy. Saproxylic beetles and wood-inhabiting fungi as obligate saproxylic species were additionally affected by tree species. In logs, the respective impact of both determinants also resulted in divergent community compositions. Finally, a rarefaction/extrapolation method was used to evaluate the effectiveness of different combinations of tree species and sun exposure for the conservation of saproxylic species diversity. Based on this procedure, a combination of broadleaved and coniferous as well as hard- and softwood tree species was identified to support preferably high levels of saproxylic species diversity.

The aim of chapter III was to evaluate the individual conservational importance of tree species for the protection of saproxylic beetles. For this, the list of tree species sampled for saproxylic beetles was increased to 42 different tree species. The considered tree species represented large parts of taxonomic and phylogenetic diversity native to Central Europe as well as the most important non-native tree species of silvicultural interest. Freshly cut branches were set up for one year and saproxylic beetles were reared afterwards for two subsequent years.

The study revealed that some tree species, in particular *Quercus* sp., host a particular high diversity of saproxylic beetles, but tree species with a comparatively medium or low overall diversity were likewise important for red-listed saproxylic beetle species. Compared to native tree species, non-native tree species hosted a similar overall species diversity of saproxylic beetles but differed in community composition.

In chapter IV, I finally analysed the interactions of host beetle diversity and the diversity of associated parasitoids by using experimentally manipulated communities of saproxylic beetles and parasitoid Hymenoptera as a model system. Classical approaches of species identification for saproxylic beetles were combined with DNA-barcoding for parasitoid Hymenoptera. The diversity of the host communities was inferred from their phylogenetic composition as well as differences in seven functional traits. Abundance, species richness, and Shannon-diversity of parasitoid Hymenoptera increased with increasing host abundance. However, the phylogenetic and functional dissimilarity of host communities showed no influence on the species communities of parasitoid Hymenoptera. The results clearly indicate an abundance-driven system in which the general availability, not necessarily the diversity of potential hosts, is decisive.

In summary, the present thesis corroborates the general importance of deadwood heterogeneity for the diversity of saproxylic species by combining different experimental approaches. In order to increase their efficiency, conservation strategies for saproxylic species should generally promote deadwood from different tree species under different conditions of sun exposure on landscape-level in addition to the present enrichment of a certain deadwood amount. The most effective combinations of tree species should consider broadleaved and coniferous as well as hard- and softwood tree species. Furthermore, in addition to dominant tree species, special attention should be given to native, subdominant, silviculturally unimportant, and rare tree species.

Zusammenfassung

Einflussfaktoren auf xylobionte Artenvielfalt und Rückschlüsse für den Naturschutz

Während der letzten Jahrhunderte hat die anthropogene Nutzung das Erscheinungsbild der Waldökosysteme in Europa grundlegend verändert. Stetig wachsende und wandelnde Ansprüche führten zu einem enormen Rückgang ökologischer Schlüsselelemente und einer strukturellen Homogenisierung der meisten Wälder. In der Folge kam es zu Rückgängen vieler waldbewohnender und insbesondere xylobionter, d.h. von Totholz abhängigen, Arten. Um dieser Entwicklung entgegenzuwirken, wurden verschiedene Schutzstrategien entwickelt, welche jedoch vor allem auf eine quantitative Totholzanreicherung abzielen. Die Vielfalt xylobionter Arten wird aber weiterhin durch unterschiedliche abiotische und biotische Einflussfaktoren sowie durch Wechselwirkungen zwischen den Arten beeinflusst. Ein detailliertes Verständnis der genauen Vorgänge fehlt jedoch bislang größtenteils. Ziel der vorliegenden Promotionsarbeit war es deshalb, das diesbezüglich bestehende Wissen zu verbessern, um die Basis für evidenzbasierte und angepasste Naturschutzmaßnahmen zu schaffen.

In Kapitel II dieser Arbeit habe ich zunächst den Einfluss der Besonnung und Baumart sowie deren Kombination im Vergleich auf xylobionte Käfer, holzbesiedelnde Pilze und Spinnen untersucht. Für die zugehörige Studie wurden dabei Stämme und Äste von sechs Baumarten bei unterschiedlicher Besonnung in einem experimentellen Ansatz ausgebracht. Der Einfluss der Besonnung und Baumart unterschied sich deutlich zwischen den einzelnen Artengruppen und Totholzdurchmessern. Alle Artengruppen wurden durch die Besonnung beeinflusst, wobei Besonnung im Vergleich zur Beschattung durch Baumkronen bei allen Artengruppen an Stämmen zu einer höheren alpha-Diversität führte und zu einer niedrigeren alpha-Diversität von xylobionten Käfern in Ästen. Xylobionte Käfer und holzbesiedelnde Pilze als obligat xylobionte Arten wurden weiterhin von der Baumart beeinflusst. Für die Artengruppen an Stämmen führten die jeweiligen Auswirkungen von Besonnung und Baumarten ebenfalls zu Unterschieden in der Zusammensetzung der Artgemeinschaften. Abschließend wurden Art-Akkumulationskurven genutzt, um die Effektivität unterschiedlicher Kombinationen aus Baumart und Besonnung für den Erhalt der xylobionten Diversität zu evaluieren. Um eine möglichst hohe Artenvielfalt zu fördern, wurde darauf basierend eine Kombination aus Laub- und Nadelholz einschließlich Weich- und Hartholzarten identifiziert.

Ziel meiner Studie in Kapitel III war es den individuellen Beitrag einzelner Baumarten zum Schutz xylobionter Käfer zu identifizieren. Dafür wurde die Zahl untersuchter Baumarten auf 42 erhöht. Die untersuchten Baumarten umfassten dabei große Teile der taxonomischen und

phylogenetischen Diversität, die in Mitteleuropa heimisch ist, sowie die wichtigsten, nicht-heimischen Baumarten von waldbaulichem Interesse. Frisch geschnittene Äste wurden für ein Jahr ausgebracht und xylobionte Käfer im Anschluss für zwei aufeinanderfolgende Jahre ausgezüchtet. Im Rahmen der Studie konnte gezeigt werden, dass einige Baumarten, insbesondere *Quercus* sp., eine besonders hohe Artenvielfalt aufweisen, aber auch Arten mit einer vergleichsweise geringen Gesamtartenzahl für Arten der Roten Liste von Bedeutung sind. Nicht-heimische Baumarten beherbergten insgesamt keine geringere Artenvielfalt von xylobionten Käfern, unterschieden sich aber in der Zusammensetzung ihrer Artgemeinschaften.

Die Studie in Kapitel IV analysiert schließlich die Wechselwirkungen zwischen Wirtsdiversität und der Diversität assoziierter Parasitoide unter Verwendung experimentell manipulierter Gemeinschaften von xylobionten Käfern und parasitoiden Hymenopteren als Modellsystem. Klassische Ansätze zur Artidentifizierung für xylobionte Käfer wurden dabei mit DNA-Barcoding für die parasitoiden Hymenopteren kombiniert. Die Vielfalt der Wirtsgemeinschaften wurde aus ihrer phylogenetischen Zusammensetzung sowie Unterschieden in sieben funktionellen Merkmalen abgeleitet. Abundanz, Artenvielfalt und Shannon-Diversität nahmen mit zunehmender Abundanz der Wirte zu. Hingegen zeigten die phylogenetische und funktionelle Ähnlichkeit der Wirtsgemeinschaften insgesamt keinen Einfluss auf die Artgemeinschaften der parasitoiden Hymenopteren. Die Ergebnisse weisen damit klar auf ein abundanz-getriebenes System hin, in dem die generelle Verfügbarkeit und nicht unbedingt die Diversität potentieller Wirte entscheidend ist.

Zusammenfassend betont die vorliegende Promotionsarbeit durch die Kombination verschiedener experimenteller Ansätze die generelle Bedeutung der Totholzheterogenität für die Vielfalt xylobionter Arten. Um ihre Effizienz zu steigern, sollten Schutzstrategien für xylobionte Arten neben einer bestimmten Totholzmenge daher generell Totholz verschiedener Baumarten bei unterschiedlicher Besonnung auf Landschaftsebene anreichern. Die effektivsten Baumarten-Kombinationen sollten dabei Laub- und Nadelholz sowie Weich- und Hartholzarten berücksichtigen. Neben den dominierenden Baumarten sollte zudem ein besonderes Augenmerk auf heimischen, subdominanten, wirtschaftlich irrelevanten und seltenen Baumarten liegen.

Chapter I: General introduction

Globally, forests are the dominant terrestrial ecosystem and fulfil a key role in safeguarding ecosystem functions and maintaining biodiversity by storing vast amounts of carbon, regulating global climate, and hosting the majority of terrestrial species (Forests Europe, 2020; Pan *et al*., 2011; Valentini *et al*., 2000; Vie *et al*., 2009). Moreover, forests provide a multiplicity of functions to humanity, including the production of timber and fuel wood, nourishments as well as recreational and cultural functions (Brockerhoff *et al.*, 2017; IPBES, 2019; Lassauce *et al*., 2012; van der Plas *et al.*, 2017). However, the continuously amplified land use pressure driven by increasing human demands and corresponding ecosystem modifications have been identified as major drivers constraining forest ecosystems and associated biodiversity (IPBES*, 2019;* Newbold *et al*., 2015; Rockström *et al*., 2009; Sala *et al*., 2000; Seibold *et al*., 2019a). Therefore, a detailed understanding of species and ecosystem processes in forests is required to derive effective conservation strategies and concepts for a sustainable utilization of forest resources.

I.1 Historical development and current situation of forest ecosystems in Europe

The current appearance of most forest ecosystems in Europe corresponds only to a small extent to their natural origin. After roughly 5000 years of human exploitation, only 0.7 % of European forest area can be considered as primeval forest remnants without any traceable anthropogenic modifications (Sabatini *et al*., 2018). Such primeval forests are composed by the natural community of tree species and characterized by a continuous small-scale mosaic of successional stages (Lachat & Müller, 2018). Furthermore, the natural development of primeval forests is shaped by natural disturbances (i.e. windthrows, forest fires, or insect outbreaks), resulting in highly diverse deadwood structures and deadwood amounts, ranging in mean from 60-90 m^3/ha in boreal to 130 m^3/ha in temperate forest ecosystems (Christensen *et al*., 2005; Siitonen, 2001). However, since the settlement of the first agricultural societies, these conditions were gradually altered, leading to massive habitat restrictions and declines of many forest-dwelling species (Grove, 2002; Lachat & Müller, 2018; Paillet *et al*., 2010; Seibold *et al*., 2019a; Speight, 1989) (Figure I.1).

Beginning from the lowland riparian forests, the degradation and fragmentation of forest ecosystems in Europe is a profound and well-documented process (Kirby & Watkins, 2015). Initially, the first human interventions initially led to an opening of landscape structures and a simultaneous increase of biodiversity. However, due to the exponential growth of human population during the following centuries, the processes of transformation and deforestation strongly accelerated (Kaplan *et al.*, 2009; Varfolomeyev & Gurevich, 2001). Before Christ, the increasing demand for wood as well as the spread of farmland already resulted in the first regional decline and extinction of forest-dwelling species, e.g. the wrinkled bark beetle (*Rhysodes sulcatus*) (Speight, 1989). The remaining forests had to satisfy versatile requirements including the use for wood pasture, pollarding, litter raking, and wood sampling (Vera, 2000). Hence, several silvicultural regimes, such as coppice or coppice with standards, evolved, combining these requirements, whereby still offering a high variety of ecological niches. Different tree species such as oak (*Quercus* sp.) were considerably supported, while other tree species like yew (*Taxus baccata*) were reduced by targeted extraction. Further development and industrial revolution led to a large-scale deforestation of several European regions (Kaplan *et al.*, 2009). As a result of overexploitation, forests were reduced in the middle of the 18th century to their smallest extent after the last glacial period (Whitehouse, 2006). The remaining forest areas were strongly fragmented and mainly located on pure soils and areas of rough topography, inappropriate for other forms of usage (Kaplan *et al.*, 2009). In consequence of declining wood production, several ideas of a modern, sustainable forest management developed to stop deforestation and ensure the long-term supply of wood (Arndt, 1815; von Carlowitz, 1713). Large old trees and deadwood, which were formerly widespread, were now called to be removed, as they were perceived as a negative element of forest ecosystems, indicating mismanagement, negligence, and waste of economic resources (Cotta, 1865; Hartig, 1808). They were also considered to promote forest diseases and disturbances, especially insect pests and forest fires, which ought to be prevented. In most silvicultural regimes, nearly every piece of wood was henceforth utilized, while large deadwood was extracted and small pieces and logging residues were directly burnt on site (Merganicova *et al.*, 2012). In Europe, the maintenance of such hygienic standards was a common practice for more than 200 years. As a result, the amount of deadwood in forests was reduced to an average of ~10m^3/ha today, representing not more than 10 to 20 % of the natural deadwood amount (Müller & Bütler, 2010). With the recent increase in wood-fuel prices, the pressure on deadwood and logging residues, even of small diameter, has increased again (Jonsell, 2007; Lassauce *et al.*, 2012). Furthermore, salvage logging remains a standard management practice following natural disturbances in most parts of the world, even in forests that are excluded from conventional logging (Müller *et al.*, 2019).

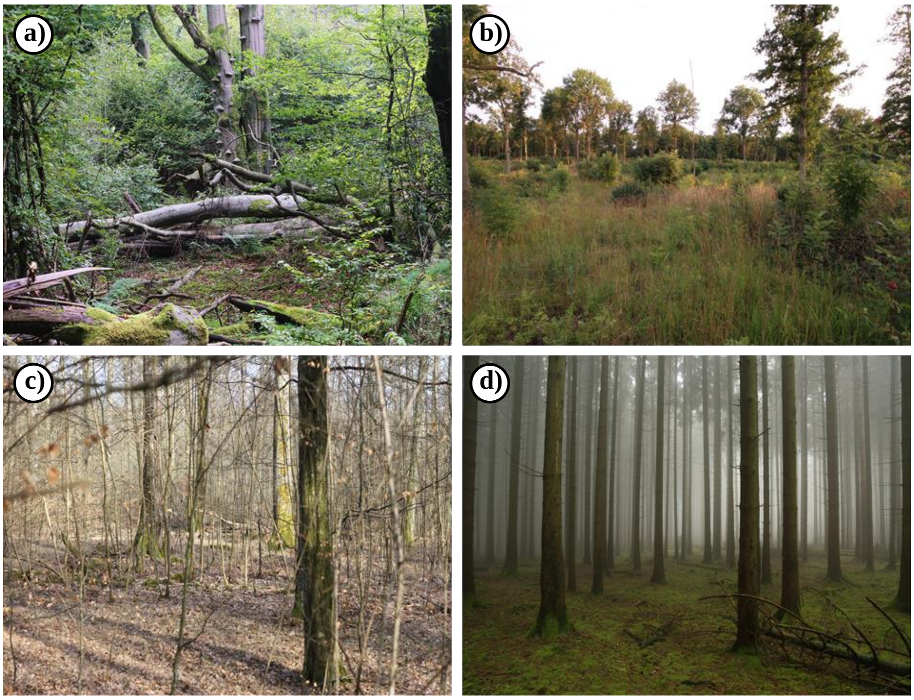

Figure I.1: Different stages of historical forest development in Europe: **a)** primeval beech forest, **b)** coppice with standards, **c)** conventionally managed forest, and **d)** monoculture of coniferous trees. The general ecological value for forest-dwelling and saproxylic species decreases from a) to d).

Another strategy to enhance wood production was the establishment of plantation forests since the 19th and 20th century (Savill, 2015). Profitable and fast-growing coniferous tree species, such as Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*), were commonly used outside their natural distributions for the afforestation of clearcuts as well as replacement of species-rich broadleaved forests by monocultures (McGrath *et al.*, 2015; Schelhaas *et al.*, 2003). These tree species partially enabled logging regimes of ~80 years compared to 150-200 years in the case of oak or European beech (*Fagus sylvatica*). Additionally, a variety of frugal, non-native tree species, such as Douglas fir (*Pseudotsuga menziesii*) or black locust (*Robinia pseudoacacia*), were introduced or planted on large scale to open new opportunities for forestry, as they partially seem to be more resistant against pathogens and pests as well as extreme climate conditions (Brus *et al.*, 2019; Krumm & Vitkova, 2016; Richardson & Rejmánek, 2011; Schmid *et al.*, 2014; Vítková *et al.*, 2017). Due to the establishment of plantation forests, the forest area in Europe slightly re-increased between 1948 and 1995 by around 10 %, while the growing stock in European forests increased accordingly by more than 200 % (Schelhaas *et al.*, 2003). A darkening of forests was further reinforced by the transformation of most traditional silvicultural regimes to modern production forests, which have mainly a permanent, uniform forest cover (Brunet *et al.*, 2012; Vollmuth, 2021). The lack of sun-exposed forest structures caused massive declines of forest-dwelling species adapted to sun-exposed conditions or to appropriate successional stages (Miklín *et al*., 2018; Müllerová *et al*., 2015).

Consequently, past and current human interventions collectively resulted in a strong fragmentation and isolation of forest ecosystems, a massive decline of ecological key elements, and a homogenization of tree species and conditions of sun exposure.

I.2 Biodiversity in deadwood

With about 70 % of the total plant biomass on earth, wood provides almost unrestricted habitats for species that live on, in, or from wood (Bar-On *et al*., 2018). Hence, the occurrence of first woody plants in the early Devonian resulted in a parallel diversification of wood-dependent species, comparable to the diversification of herbivores with the evolution of flowering plants (Ulyshen & Sobotnik, 2018). Species which are particularly linked to the decay of wood are termed as saproxylic and encompass "species which are involved in or dependent on the process of fungal decay of wood, or on the products of that decay, and which are associated with living as well as dead trees" (Alexander, 2008). Saproxylic species fulfil the essential role of deadwood decomposition and thus recycling of nutrients in forest ecosystems (Seibold *et al*., 2021; Stokland *et al*., 2012). Among saproxylic species, arthropods and wood-inhabiting fungi account for the majority of species diversity, but also parts of other taxa like bacteria or birds are contributing (Stokland *et al*., 2012). Even a large variety of non-saproxylic species, e.g. amphibians, molluscs, plants, and lichens are benefiting from deadwood as a shelter and a source of nutrients (Spribille *et al*., 2008; Szewczyk & Szwagrzyk, 1996). The global and regional number of saproxylic species is recently unknown due to the inaccuracy of total biodiversity measurements and the lack of information regarding the life-history of single species (Stokland *et al*., 2012). For northern Europe, however, cautious estimates assume that 20 to 25 % of all forest-dwelling species are saproxylic (Siitonen, 2001), whereby evaluations of single taxa indicate similar or even higher proportions for Central Europe (Köhler, 2000).

Due to the massive modifications of forest ecosystems by past human practices, saproxylic species have become one of the most threatened groups in Europe and beyond, as many of them are highly sensitive to changes in deadwood abundance and diversity (Seibold *et al*., 2016b; Ulyshen & Hanula, 2009). Even if the European Red List of saproxylic beetles evaluates only a small subset of species, approximately 24 % are classified as threatened or near threatened, while 48 % are non-threatened (least concern) (Cálix *et al*., 2018). In comparison, the comprehensive Red List of saproxylic beetle species of Germany classifies more than 40 % of all saproxylic beetle species as threatened or higher (Schmidl & Büche, 2019). The extinction risk of single saproxylic beetle species mirrors well the historic development of European forests. As revealed by Seibold *et al*. (2015b) species of lowland regions, large species as well as species that depend on large deadwood diameters, broadleaved tree species, and sun-exposed conditions are particularly affected. Due to their sensitivity, different saproxylic species are considered indicators for forest degradation (Buse, 2012; Cateau *et al*., 2018; Eckelt *et al*., 2018; Lachat *et al*., 2012) and are guiding conservation laws and programs like the Habitats Directive of the European Union (EWG, 1992).

The habitat suitability for saproxylic species is linked to a variety of different abiotic and biotic determinants (reviewed in Seibold *et al*., 2015a), whereby many species exhibit clear preferences (e.g. Buse *et al*., 2008; Kašák *et al*., 2019; Kostanjsek *et al*., 2018). In modern production forests, these determinants are strongly restricted by intensive management regimes (Seibold *et al*., 2015b). The amount of deadwood has an important but subordinate role compared to that of deadwood heterogeneity (Seibold *et al*., 2016b), even as both are often correlating under natural conditions (Müller & Bütler, 2010). Beside determinants such as the deadwood diameter (Brin *et al*., 2011; Buse *et al*., 2008; Heilmann-Clausen & Christensen, 2004; Kostanjsek *et al*., 2018) the deadwood position and deadwood type (e.g. standing/lying, forest floor/canopy, snag/log) (Bouget *et al*., 2012; Hjältén *et al*., 2010; Lindhe *et al*., 2004), the occurrence of saproxylic species is substantial determined by the host tree identity and microclimatic conditions (Krah *et al*., 2018; Seibold *et al*., 2016b). Like phytophagous species, saproxylic species can vary from being largely polyphagous, colonising a variety of different tree species, to being monophagous and thus restricted to a single host tree species (Dahlberg, & Stokland, 2004; Junninen & Komonen, 2011; Klausnitzer *et al*., 2018; Milberg *et al*., 2014). Current studies revealed especially a more or less distinctive separation between saproxylic communities of broadleaved and coniferous tree species (Dahlberg, & Stokland, 2004; Junninen & Komonen, 2011; Purahong *et al*., 2018a; Wu *et al*., 2008). Host tree specificity furthermore decreases with ongoing decomposition (Wu *et al*., 2008; Zuo *et al*., 2021), while species colonising early successional stages reveal the highest specificity as well as xylophagous species reveal a higher specificity compared to mycetophagous or zoophagous species (Wende *et al*., 2017). The microclimatic conditions are primarily determined by canopy closure, which correlates with differences in humidity and temperature (Chen *et al*., 1999; Scharenbroch & Bockheim, 2007; Seibold *et al*., 2016a; Thom *et al*., 2020), but can also be influenced by the activity of saproxylic species itself (Ulyshen, 2016). Saproxylic invertebrates often reveal a higher abundance and diversity under sun-exposed conditions as well as a preference for such conditions, particular a variety of threatened saproxylic beetle species (Jonsell *et al*., 1998; Lindhe *et al*., 2005; Seibold *et al*., 2015b; Seibold *et al*. 2016a). Also the decomposition activity of wood-inhabiting fungi highly depends on humidity and temperature (Venugopal *et al*., 2016). Sun exposure seems to affect deadwood of smaller diameters much stronger, as larger logs seem to better buffer the effects of microclimatic extremes (i.e. heat, drought) (Bässler *et al*., 2010b; Siitonen & Ranius, 2015). Collectively, however, most studies investigating the impact of different determinants of saproxylic species are revealing three major deficiencies (reviewed in Seibold *et al*., 2015a). First, the majority of knowledge is based on occasional observations or field surveys (e.g. Bense, 1995; Hellrigl, 1978a, 1978b; Klausnitzer *et al*., 2018; Palm, 1959), whereas experimental approaches under standardized and replicable conditions are scarce, thus limiting precise statements. Moreover, these studies are limited in their extent, e.g. by the number of investigated tree species. Comparisons were done in a range of 2 to 20 tree species, but only incorporating the most common, regionally dominant, or silviculturally important tree species, while large parts of woody plant diversity are neglected (Andringa *et al*., 2019; Lindhe *et al*., 2005; Müller *et al*., 2015b; Saint-Germain *et al*., 2007). Lastly, studies investigating determinants of saproxylic species diversity are rarely focusing on more than one determinant. However, the partial impact of single determinants is likely to deviate, in particular between different saproxylic taxa, and single determinants possibly interact with each other.

Deadwood as a complex and ephemeral resource offers a multiplicity of different niches for saproxylic species and lifestyles (Stokland *et al*., 2012). The saproxylic food web is mainly based on wood-inhabiting fungi and bacteria, which are colonising wood rapidly after die-off or are already present as endophytes (Song *et al*., 2017; Vogel *et al*., 2017). Their enzymatic activity is mainly responsible for the chemic decomposition of wood by degrading cellulose, hemicellulose and lignin (Stokland *et al*., 2012). In contrast, the occurrence of saproxylic invertebrates promotes the mechanic destruction of wood (Ulyshen, 2016). The highly complex saproxylic food web is completed by species-rich predators, parasites, and parasitoids (Hilszczański, 2018; Stokland *et al*., 2012). Nevertheless, studies on saproxylic species are mostly focussing on saproxylic beetles, basidiomes of wood-inhabiting fungi, and spiders, while more cryptic taxa like parasitoid Hymenoptera are underrepresented and thus not considered within conservation strategies by ignoring their contribution to the saproxylic species diversity (Hilszczański, 2018; Shaw & Hochberg, 2001; Stokland *et al.*, 2012). In this regard, however, rapidly developing molecular methods have recently generated new opportunities of species identification (Hebert *et al.*, 2003; Ratnasingham & Hebert, 2007, 2013). This development also enables the quantification of interactions among different trophic levels. In the saproxylic food web such analyses have been barely applied except for fungus-fungus-systems and fungus-beetle-systems, revealing a large variety of horizontal and vertical interactions (Fukami *et al.*, 2010; Seibold *et al.*, 2019b; Six, 2012; Skelton *et al.*, 2020). Nevertheless, interactions between higher trophic levels, as in a host-parasitoid-systems, remain so far largely unknown.

I.3 Conservation of saproxylic biodiversity

The importance of deadwood and deadwood structures for a variety of species was already recognized by naturalists of the 19th and ecologists in the early 20th century (Graham, 1925; Mölder *et al.*, 2020; Thomas, 2002; Wallace, 1869). However, it took until the late 1980s before this importance was broadly recognized for the conservation of European forests and not only considered by the protection of habitat trees for nesting birds or bats (Mölder *et al.*, 2020; Speight, 1989). Within the last three decades, deadwood ecology has now grown as an own discipline and a multiplicity of scientific articles have been published that demonstrate the linkage between losses of deadwood and declines in biodiversity (Stokland *et al.*, 2012). Due to this large progress, deadwood is nowadays implemented into various monitoring programs, conservation strategies, and certification schemes all over the world, e.g. FSC and PEFC. The strategies of conservation can thereby be classified in terms of their focus on the reservation, retention, and restoration of forest ecosystems (Brunet *et al.*, 2010).

In large protected areas, e.g. national parks, a benign-neglect concept is mostly applied, where deadwood is generally not removed after natural disturbances (Müller *et al.*, 2010). This strategy accounts for the importance of early successional stages and deadwood legacies as well as heterogeneous deadwood structures for biodiversity (Hilmers *et al.*, 2018; Swanson *et al.*, 2011). In Europe only ~ 4 % of the forest area are set aside exclusively for conservation (including large protected areas, smaller conservation areas, and forest reserves), while ~ 24 % are under some kind of protection for biodiversity, and approximately ~ 96 % are subjected to some kind of commercial forest management (Forest Europe, 2020; Lindenmayer *et al.*, 2012a). However, currently existing forest areas set aside exclusively for conservation seem to be insufficient to conserve stable populations of saproxylic species alone, as they are often small or spatially isolated (Bollmann & Braunisch, 2013; Bouget & Parmain, 2016; Hallmann *et al.*, 2017) and the potential to set aside more areas is furthermore limited by commercial and societal demands. Therefore, the additional integration of conservation measures in managed forests is often proposed as a strategy for an effective conservation (Bauhus *et al*., 2009; Bonsu *et al*., 2017; Kraus & Krumm, 2013; Maier & Winkel, 2017), which is also confirmed by case studies from the Steigerwald forest, Germany (Doerfler *et al*., 2017; Leidinger *et al*., 2020; Roth *et al*., 2019).

Integrative conservation strategies can be basically divided into passive and active approaches of deadwood enrichment. Passive approaches mainly include the retention of forest patches, tree groups, or single trees, frequently by considering microhabitat structures (Gustafsson *et al*., 2020a, 2020b; Kraus *et al*., 2016; Mölder *et al*., 2020; Vítková *et al*., 2018). However, rates of deadwood enrichment within passive approaches are initially slow, especially in young, formerly managed stands, as deadwood is only accumulated by the natural succession and senescence of trees (Holzwarth *et al*., 2013; Oheimb *et al*., 2007; Vandekerkhove *et al*., 2009). By contrast, active approaches can help to reach specific thresholds of deadwood in a comparably shorter period of time. Hence, combinations of passive and active approaches are considered as suitable solutions for deadwood enrichment (Vítková *et al*., 2018). Such active approaches include the leaving of tree parts, e.g. treetops, logs of poorer quality, or high stumps after harvest operations, and also the active creation of deadwood by different methods, such as tree veteranisation, girdling, pollarding, felling, and pulling (Brandeis *et al*., 2002; Cavalli & Mason, 2003; Sebek *et al*., 2013; Sillett *et al*., 2018), the active creation of microhabitats by chainsaw (Zapponi *et al*., 2015) as well as prescribed burning (Heikkala *et al*. , 2017). Such artificially created deadwood appears to be of similar habitat quality for saproxylic species compared to deadwood created by natural dynamics, while different techniques are recommended to be combined to guarantee a high heterogeneity of deadwood structures (Pasanen *et al*., 2018).

Although integrative strategies try to combine economic and ecological demands, most of these previous strategies of deadwood enrichment solely focus on the deadwood quantity, since that is financially more significant, while deadwood heterogeneity is only named as a general aim or more or less neglected, with a few exceptions like the Contract-Based Conservation Program of Forests in Bavaria (StMUV & StMELF, 2021). Most strategies aim at reaching critical thresholds of 20 to 50 m^3/ha and additionally 3 to 10 habitat trees/ha of regionally dominant broadleaved tree species (mostly *F. sylvatica*) under prevalent shaded conditions by neglecting subdominant, silviculturally unimportant, or rare tree species as well as sun-exposed conditions (Thorn *et al*., 2018b). In general, such an increase of deadwood amount shows all in all positive effects, even on many non-saproxylic species (Seibold *et al*., 2016a; Ulyshen *et al*., 2011), but deadwood heterogeneity is at least of similar importance for restoring natural saproxylic communities (Seibold *et al*., 2016b). Hence, an ecologically sustainable forest management requires the recovery of the natural deadwood amount but also different facets of deadwood heterogeneity. Moreover, the integration of deadwood heterogeneity can increase the effectiveness of conservation strategies, even in an economic perspective, as a higher deadwood heterogeneity is able to compensate lower deadwood amounts and thus to compensate the financial effort (Müller *et al*., 2015a; Seibold *et al*., 2016b). Unfortunately, the guidance of how to integrate deadwood heterogeneity into forest management is lagging behind, as scientific knowledge is partially insufficient (Seibold *et al*., 2015a; Vítková *et al*., 2018) (see I.2), and the financial attraction of federal conservation programs is not always given (see however StMUV & StMELF (2021)). Only a small number of previous studies tried to give applicable recommendations with targeted instructions (reviewed in Vítková *et al*., 2018) that only require a minimum of additional effort. Recommendations about which tree species and combinations most effectively support the highest diversity of saproxylic beetles, wood-inhabiting fungi, and other saproxylic taxa are for instance provided by Andringa *et al*. (2019), Gossner *et al*.(2016), and Purahong *et al*. (2018a), comparing 20, 13, and 11 tree species under uniform conditions of sun exposure. Those studies identified a high diversity of saproxylic species for instance in relation to hornbeam (*Carpinus betulus*) and *P. abies*. Nevertheless, comprehensive recommendations under inclusion of different determinants of saproxylic species are so far lacking, making further investigations necessary.

I.4 Main objectives

The main objectives of this thesis were to improve the understanding of different determinants and processes shaping the diversity of saproxylic species and simultaneously to provide evidence-based and applicable recommendations for the improvement of conservation strategies in forest ecosystems by using experimental approaches.

In chapter II, I focussed on the impact of sun exposure, tree species, and their combination on saproxylic beetles, wood-inhabiting fungi, and spiders of early decay. For this study, logs and branches of six tree species were set up under three sun exposure treatments. Moreover, I assessed different combinations of sun exposure treatments and tree species with regard to their effectiveness for deadwood enrichment.

In chapter III, I expanded the list of tree species experimentally sampled for saproxylic beetles by investigating branches of 42 different tree species. These tree species represent large parts of the taxonomic and phylogenetic diversity distributed in Central Europe as well as the most important non-native tree species of silvicultural interest. The aim of chapter III was to provide a detailed insight into the occurrence of saproxylic beetles across multiple tree species and to quantify the individual importance of single tree species for the conservation of saproxylic beetles.

In chapter IV, I analysed the interactions between host diversity and the diversity of associated parasitoids by using experimentally manipulated communities of saproxylic beetles and parasitoid Hymenoptera as a model system. To identify parasitoids and the respective hosts I combined classical approaches of species identification for saproxylic beetles with DNA-barcoding for parasitoid Hymenoptera. The taxonomic, functional, and phylogenetic diversity of hosts were taken into account to draw initial conclusions about trophic interactions in the saproxylic food web.

Chapter II: Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach

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II.1 Abstract

(1) The enrichment of deadwood is essential for the conservation of saproxylic biodiversity in managed forests. However, existing strategies focus on a cost-intensive increase of deadwood amount, while largely neglecting increasing deadwood diversity.

(2) Deadwood objects, i.e. logs and branches, from six tree species were experimentally sun-exposed, canopy-shaded and artificially shaded for 4 years, after which the alpha-, beta-, and gamma-diversity of saproxylic beetles, wood-inhabiting fungi, and spiders were analysed. Analyses of beta-diversity included the spatial distance between exposed deadwood objects. A random-drawing procedure was used to identify the combination of tree species and sun exposure that yielded the highest gamma-diversity at a minimum of exposed deadwood amount.

(3) In sun-exposed plots, species numbers in logs were higher than in shaded plots for all taxa, while in branches we observed the opposite for saproxylic beetles. Tree species affected the species numbers only of saproxylic beetles and wood-inhabiting fungi. The beta-diversity of saproxylic beetles and wood-inhabiting fungi among logs was influenced by sun exposure and tree species, but beta-diversity of spiders by sun exposure only. For all saproxylic taxa recorded in logs, differences between communities increased with increasing spatial distance.

(4) A combination of canopy-shaded *Carpinus* logs and sun-exposed *Populus* logs resulted in the highest species numbers of all investigated saproxylic taxa among all possible combinations of tree species and sun-exposure treatments.

(5) *Synthesis and applications*. We recommend incorporating the enrichment of different tree species and particularly the variation in sun exposure into existing strategies of deadwood enrichment. Based on the results of our study, we suggest to combine the logs of softwood broadleaved tree species (e.g. *Carpinus, Populus*), hardwood broadleaved tree species (e.g.

Quercus), and coniferous tree species (e.g. *Pinus*) under different conditions of sun exposure and distribute them spatially in a landscape to maximize the beneficial effects on overall diversity.

II.2 Introduction

Past practices of intensive forest management have resulted in a massive decline in key ecological elements, such as dead and moribund trees (Thorn *et al*., 2020; Whitehouse, 2006). In addition, with the recent increase in wood-fuel prices, the pressure on deadwood and logging residues, even of small diameter, has increased (Lassauce *et al*., 2012).

In Europe, at least 20–30 % of all forest-dwelling species are regarded as saproxylic, i.e. dependent on deadwood (e.g. many species of beetles and fungi) or able to use it facultatively, for example as shelter or as a foraging substrate (e.g. epixylic spiders) (Siitonen, 2001). Saproxylic organisms are important drivers of wood decomposition and nutrient cycling (Alexander, 2008; Ulyshen, 2016), but with large-scale declines in deadwood amount many species have become endangered or extinct (Seibold *et al*., 2015b).

The local alpha-diversity of saproxylic organisms is determined by several environmental drivers operating at the scale of a single deadwood object (Seibold *et al*., 2015a) and mainly determined by object type (e.g. snag/log/branch, laying/standing), microclimate, tree species, and decomposition stage (Gossner *et al*., 2016; Krah *et al*., 2018). In addition, communities of saproxylic organisms differ between deadwood of different diameters (Heilmann-Clausen & Christensen, 2004; Pouska *et al.*, 2011). The microclimatic conditions of deadwood objects are mainly determined by canopy openness, which correlates with differences in humidity and temperature (Chen *et al.*, 1999; Scharenbroch & Bockheim, 2007; Seibold *et al.*, 2016 a, 2016b). For instance, within communities of saproxylic beetles and spiders the highest species numbers are typically reached on sun-exposed deadwood (Müller *et al.*, 2015a; Thorn *et al.*, 2016a), whereas wood-inhabiting fungi prefer sites where the humidity is higher (Bässler *et al.*, 2010b). Finally, the local characteristics of deadwood typically differ among different forest stands, which together with species-specific dispersal abilities cause a spatial turnover of community composition of saproxylic organisms (Komonen & Müller, 2018; Schall *et al*., 2018). Under natural conditions, the occurrence of particular tree species often correlates with the degree of sun exposure impeding the unravelling of the decisive factors for the diversity of saproxylic organisms in observational field studies (Seibold *et al.*, 2015a). Hence, a complete understanding of the environmental drivers of species beta-diversity, which together with alpha-diversity determines the total gamma-diversity, is lacking.

Integrative conservation strategies incorporating deadwood enrichment have been implemented within the last 20 years (Vítková *et al*., 2018) and are mainly of two types. The first involves the passive enrichment of deadwood by terminating production in a forest stand and designating it as a protected area or by protecting single habitat trees and tree groups (Lindenmayer & Laurance, 2017; Vítková *et al*., 2018). This results in the accumulation of deadwood by natural processes, such as disturbances or natural senescence. A passive enrichment encompasses both, sun-exposed and shaded deadwood (Sebek *et al*., 2016; Vodka *et al*., 2009). The second strategy consists of the active enrichment of deadwood during harvest operations, in which deadwood is mainly created by leaving tree parts, e.g. treetops, on site (Sandström *et al*., 2019). Active strategies aim at integrating economic and ecological demands (Bauhus *et al*., 2009) and thus focus on deadwood amount rather than deadwood diversity. As a consequence, deadwood is mostly enriched under the shaded conditions of uneven-aged forests and the majority of deadwood derives from the dominant tree species, although tree species and the degree of sun exposure of enriched deadwood can be controlled during regular harvest operations (Doerfler *et al*., 2017).

In this study, we tested the role of deadwood quality for biodiversity by examining the alpha-, beta-, and gamma-diversity of saproxylic beetles and wood-inhabiting fungi, two obligate saproxylic groups that directly depend on deadwood, as well as spiders that use deadwood facultatively, i.e. as a structural component and feeding ground. In an experimental approach, all three taxa were sampled in the logs and branches of six tree species subjected to three treatments related to sun exposure. We predicted (1) higher species numbers of saproxylic beetles and spiders but lower species numbers of wood-inhabiting fungi under sun-exposed conditions, and (2) the greater importance of tree species for saproxylic beetles and wood-inhabiting fungi compared to spiders, because of their direct dependence on deadwood. We then determined which combination of tree species and sun exposure promote highest gamma-diversity.

II.3 Materials and methods

Study area and experimental design

Our study was conducted in the Steigerwald forest, located in northern Bavaria, Germany (N 49° 50´; E 10° 29´). This area covers around ~16,500 ha of forested area by a mean annual temperature of 7–8 °C and an annual precipitation of 750–850 mm (BayFORKLIM, 1996). Forest stands consist mainly of European beech (*Fagus sylvatica*, 44 %), sessile oak (*Quercus* *petraea*, 20 %), and Scots pine (*Pinus sylvestris,* 14 %). Other broadleaved tree species account for 10 % and other coniferous trees, such as Norway spruce (*Picea abies*) for 12 % of the forested area. Intensive management over a period of centuries depleted the forest of deadwood and moribund trees. However, active enrichment of deadwood has been practiced by the local forest administration since 2005 (Doerfler *et al*., 2017).

In 2015, we established six study sites, each containing three subplots differing in their levels of sun exposure (Figure II.1): (1) sun-exposed on a forest meadow, (2) canopy-shaded within a closed forest stand, and (3) artificially shaded by mesh nets on a forest meadow. The third treatment was implemented to obtain shaded conditions without any bias of co-varying factors from the forest stand.

Freshly cut logs of six different tree species were randomly exposed in early 2015 on each subplot, including two softwood broadleaved tree species: hornbeam (*Carpinus betulus*) and aspen (*Populus tremula*); two hardwood broadleaved tree species: *F. sylvatica* and *Q. petraea*; and two coniferous tree species: silver fir (*Abies alba*), and *P. sylvestris* (henceforth only the genus names is used for simplicity). All logs were felled in the study area and had a similar mean diameter of 32.9 (± 5.6) cm and a similar mean length of 303 (±10.4) cm. To prevent possible influences of ground vegetation, all logs were placed on oak logs with a diameter of 25 cm. In addition, branch-bundles of all tree species were exposed under the same treatments on each subplot from April 2016 to June 2016. The branches in the bundles had a mean length of 220.6 (± 29.4) cm and a mean diameter of 2.2 (± 0.5) cm.

Biodiversity surveys

We focused on saproxylic beetles and wood-inhabiting fungi, as both groups are important drivers of deadwood decay (Ulyshen, 2016), and spiders as facultative users of deadwood.

Communities of saproxylic beetles and spiders were sampled using stem emergence traps. This type of trap is tightly covering a given log section of a log and enables to trap all arthropods which develop or overwinter in the respective log section. Traps were filled with saturated saline solution as sampling fluid and emptied monthly between April and September in 2016, 2017, and 2018. Between years, trap positions were shifted on the logs to avoid bias due to trap coverage. Branch-bundles were reared from July 2016 to September 2017 in plastic tubes to which ethanol-filled trapping bottles had been attached (Supporting Information S1). Emerging beetles and spiders were determined by taxonomic specialists according to Freude et al. (1963–1984) and Heimer and Nentwig (1991). Beetles were classified as saproxylic according to Schmidl and Bussler (2004). Basidiomes of wood-inhabiting fungi were assessed

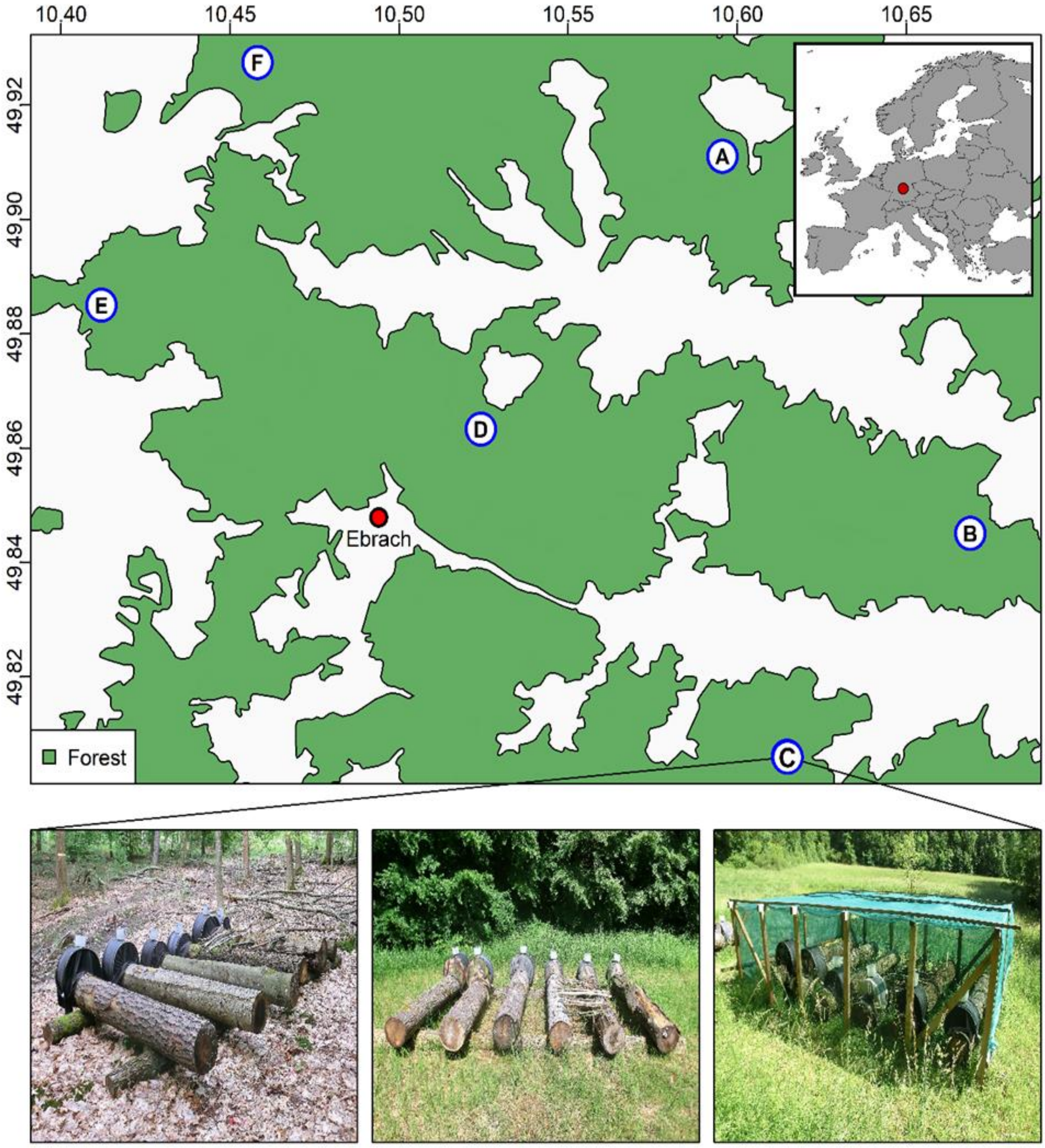

Figure II.1: Study area and experimental design. The study was conducted in the Steigerwald forest, located in northern Bavaria, Germany, at six different study sites (A–F). Each site consisted of three subplots that differed in their degree of sun exposure (from left to right): canopy-shaded within the forest stand, sun-exposed on a forest meadow, and artificially shaded by mesh nets. Freshly cut logs and branch-bundles of six tree species (*Abies alba*, *Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris*, *Populus tremula*, and *Quercus petraea*) were exposed on each subplot. Deadwood objects were sampled for saproxylic beetles, basidiomes of wood-inhabiting fungi, and spiders for three subsequent years. Forest classification is based on Corine land cover data (version 20b2).

visually on the log surfaces in October 2016, 2017, and 2018. Species were identified either in the field or, for cryptic species, in the laboratory. Because of the low numbers of records of wood-inhabiting fungi and spiders in branch-bundles, these taxa were analysed only from logs.

Data analysis

All analyses were performed using R 3.3.2 (R Development Core Team, 2019a). The effects of different treatments and tree species on alpha-diversity were tested by applying generalised linear mixed-effects models for each taxonomic group and for logs and branches separately (package `lme4´; Bates *et al*., 2015). The effects of treatment and tree species on species numbers were tested independently within two models, and the combined effects of treatment and tree species in a third model. The branch surface was added as an additional predictor to control for resource amount, while the resource amount was standardized for the logs by the respective trap area. Plot identity and year were added as random effects to all models. A linear inference procedure with the simultaneous adjustment of *p*-values was applied by means of the function `glht´ (package `multcomp´; Hothorn *et al*., 2008) to compare species numbers between treatments, tree species, and their combinations. Differences in community composition between treatments, tree species, and combinations thereof were visualized by nonmetric multidimensional scaling (package `vegan´; Oksanen *et al*., 2019).

The effects of tree species, treatment, and space on the beta-diversity were measured as Bray-Curtis dissimilarities of communities by using multiple regression on distance matrices (MRM; Lichstein, 2007) and regularized discriminant analysis (RDA; Friedman, 1989). Although MRM and Mantel tests are widely used in spatial analyses, they have less power to detect spatial autocorrelations in the response data (Legendre *et al*., 2015). RDA offers an alternative method, as in the detection of spatial structure it has a higher power than the Mantel tests used for MRM (Legendre *et al*., 2015).

For the MRM, distance matrices were generated using the function `dist´ (package `proxy´; Meyer & Buchta, 2019) and by applying: (1) a Gower distance based on the treatment of each subplot, (2) a cophenetic distance based on the phylogenetic tree of European flora provided by Durka and Michalski (2012), as a proxy of distances between different tree species, and (3) a spatial distance between each deadwood object based on the distance-based Moran`s eigenvector map (Dray *et al*., 2006). Distances in species compositions between deadwood objects were calculated as Bray-Curtis distances using the function `vegdist´ (package `vegan´; Oksanen *et al*., 2019). The MRM was applied using the function `MRM´ (package `ecodist´; Goslee & Urban, 2007).

The same distance matrices were used in the RDA, together with the treatment as a factor. Distances in species composition were calculated based on Hellinger transformed species data. The function `ANOVA´ was then applied to test the impact of treatment, tree species, and space (package `vegan´; Oksanen *et al*., 2019). Since the RDA and MRM (see

Supporting Information S8, Table 1) generated comparable results, only the RDA was used in data interpretation.

Effects of treatment and tree species and combinations thereof on gamma-diversity were compared using the rarefaction-extrapolation framework (Chao *et al*., 2014), implemented in the `iNEXT´ package (Hsieh *et al*., 2016).

Finally, the combination of tree species and sun exposure yielding the highest gamma-diversity was determined. Deadwood objects shaded by mesh nets were excluded from the analysis, since mesh treatment is not feasible as an integrative strategy to deadwood enrichment. The remaining 72 experimental deadwood objects (six plots × six tree species × sun-exposed/canopy-shaded) were subjected to random selections of 1–12 different deadwood objects (i.e. only sun-exposed deadwood objects of one tree species or up to one sun-exposed and one canopy-shaded deadwood object of each tree species). To standardize for the amount of exposed deadwood, the sampling effort was rarified to six deadwood objects (package `iNEXT´; Hsieh *et al*., 2016). The same approach was used to calculate a pooled gamma-diversity for combinations of tree species and sun exposure for all taxa associated with the logs. The possible combinations of tree species and sun exposure are listed in the Supporting Information S12–S16.

II.4 Results

Alpha-diversity

During three years of sampling, 238 species (16,264 individuals) of saproxylic beetles, 109 species of wood-inhabiting fungi, and 126 species (2,421 individuals) of spiders were identified in logs, while 57 species (2,189 individuals) of saproxylic beetles were reared from the branches (see Supporting Information S17–S20).

The species numbers of all species groups were higher in sun-exposed than in canopy-shaded logs (see Supporting Information S2). The species numbers of saproxylic beetles were lower on the artificially shaded plots than on the canopy-shaded plots, while it was adverse for wood-inhabiting fungi and no differences were detected for spiders. Tree species affected the species numbers of saproxylic beetles and wood-inhabiting fungi but not that of spiders (see Supporting Information S3). Species numbers of saproxylic beetles and wood-inhabiting fungi were highest in logs of *Carpinus*, *Fagus*, and *Populus* (Figure II.2). A comparison of single tree species showed either higher species numbers in sun-exposed logs or no differences between treatments (Figure II.3; see Supporting Information S4). A comparison of sun-exposed and canopy-shaded plots showed higher species numbers of saproxylic beetles in logs of *Abies*, *Populus*, and *Quercus*, and of wood-inhabiting fungi in logs of *Abies*, *Carpinus*, *Fagus*, and *Quercus*. The species numbers of spiders were highest in logs from the sun-exposed plots, regardless of the tree species.

The community composition of saproxylic beetles and spiders, but not of wood-inhabiting fungi, differed significantly between sun-exposed, artificially shaded, and canopy-shaded plots (see Supporting Information S5). Community composition in logs of the different tree species differed only for saproxylic beetles and wood-inhabiting fungi (see Supporting Information S6 and S7).

Lower species numbers of saproxylic beetles were found in sun-exposed branches than in artificially shaded and canopy-shaded branches (see Supporting Information S2). The species numbers of saproxylic beetles also differed between tree species (see Supporting Information S3) and were higher in branches of *Abies*, *Fagus*, and *Quercus* than in *Carpinus*, *Pinus*, and *Populus* branches. For *Carpinus* and *Pinus*, canopy-shaded branches supported a larger number of species than sun-exposed branches did (see Supporting Information S4). The community composition of saproxylic beetles did not differ between treatments or tree species (see Supporting Information S5–S7).

Beta-diversity

The beta-diversity of saproxylic beetles in logs was most strongly affected by treatment, followed by tree species and space, while the tree species was most important for wood-inhabiting fungi in logs (Table II.1). Spiders in logs were only affected by treatment and space. For saproxylic beetles reared from branches only the tree species, followed by treatment, showed an influence. Overall, an increasing number of tree species, and a larger spatial distance resulted in a higher species turnover.

Gamma-diversity

The gamma-diversity across all tree species in logs and branches did not differ between the sun-exposed, canopy-shaded, and artificially shaded subplots in any of the analysed taxa (see Supporting Information S9). For all species groups, gamma-diversity differed marginally between logs of the different tree species (see Supporting Information S10), but was significantly lower in *Pinus* branches than in branches of any of the other tree species.

A tree species specific analysis of the effects of the amount of sun exposure showed generally a lower gamma-diversity of saproxylic beetles in artificially shaded logs than in canopy-shaded logs (see Supporting Information S11). For wood-inhabiting fungi, gamma-diversity in *Carpinus* logs was lower in the canopy-shaded treatment than in either the artificially shaded or sun-exposed treatment. Spiders had a higher gamma-diversity in *Fagus* logs that were sun-exposed compared to artificially shaded logs. For saproxylic beetles, gamma-diversity was lower in the sun-exposed branches of *Carpinus* than in the artificially shaded or canopy-shaded branches of the same species.

The gamma-diversity resulting from combinations of tree species and sun exposure increased as the number of combined experimental deadwood objects increased (Figure II.4) and was highest for combinations of one to five different objects (see Supporting Information S12–S16). For saproxylic beetles in logs, gamma-diversity was highest for the combination of canopy-shaded logs of *Carpinus* and *Pinus* and sun-exposed logs of *Populus* (see Supporting Information S12). Wood-inhabiting fungi had the highest gamma-diversity in sun-exposed logs of *Populus* (see Supporting Information S13). For spiders, a combination of canopy-shaded *Pinus* and sun-exposed *Populus* logs resulted in the highest gamma diversity (see Supporting Information S14). Overall, the combination of canopy-shaded *Carpinus* and sun-exposed *Populus* logs yielded the highest species numbers of all investigated taxa in logs (see Supporting Information S15). For saproxylic beetles in branches, gamma-diversity was highest in canopy-shaded branches of *Quercus* alone (see Supporting Information S16).

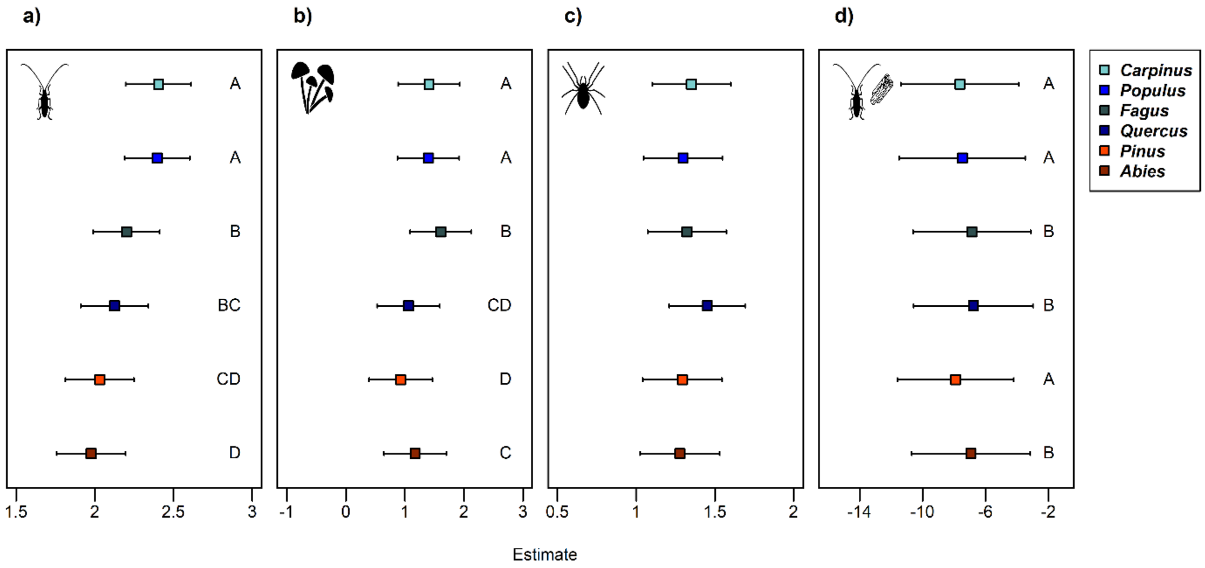

Figure II.2: Model estimates for the impact of tree species on the alpha-diversity of **a)** saproxylic beetles in logs, **b)** wood-inhabiting fungi in logs, **c)** spiders in logs, and **d)** saproxylic beetles in branches. For detailed model results see Supporting Information S3. Species were recorded in deadwood objects of six different tree species subjected to three different sun exposure treatments (sun-exposed, canopy-shaded, and artificially shaded) for three subsequent years.

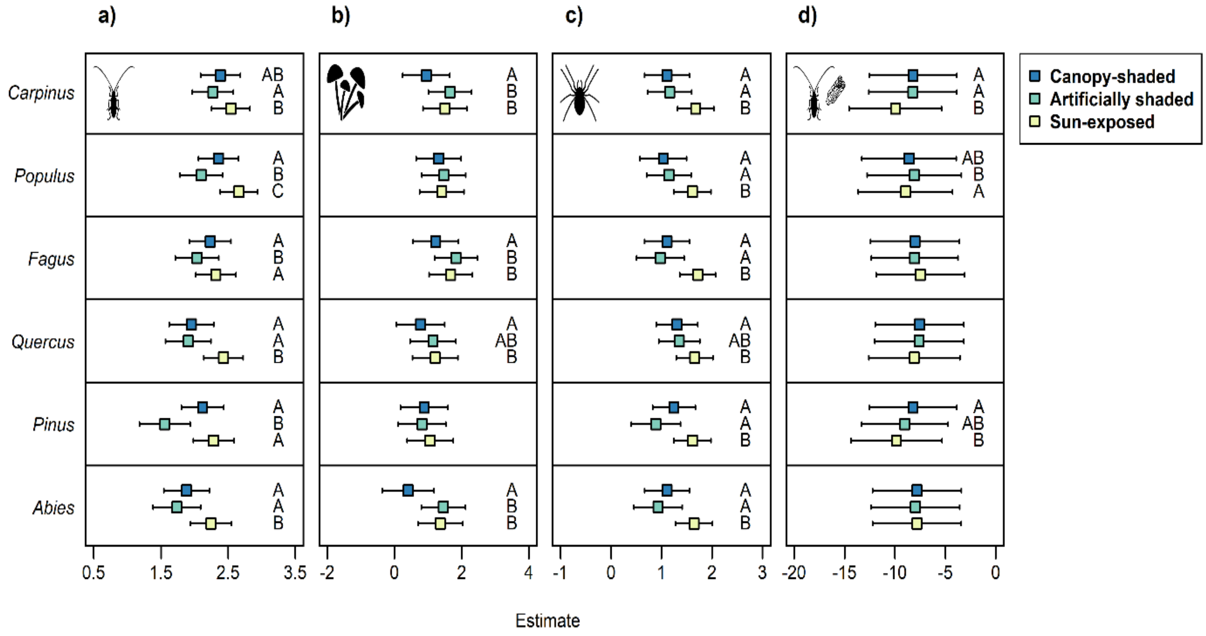

Figure II.3: Model estimates for the tree-species-specific impact of sun exposure on the alpha-diversity of **a)** saproxylic beetles in logs, **b)** wood-inhabiting fungi in logs, **c)** spiders in logs, and **d)** saproxylic beetles in branches. For detailed model results see Supporting Information S4. Species were recorded in deadwood objects of six different tree species subjected to three different sun exposure treatments for three subsequent years.

Table II.1: Effects of tree species, treatment, and space on the beta-diversity of **a)** saproxylic beetles in logs, **b)** wood-inhabiting fungi in logs, **c)** spiders in logs, and **d)** saproxylic beetles in branches as determined in a regularized discriminant analysis (RDA). Species were recorded in deadwood objects of six different tree species (*Abies alba*, *Carpinus betulus*, *Fagus sylvatica*, *Pinus sylvestris*, *Populus tremula*, and *Quercus petraea*) subjected to three different sun exposure treatments (sun-exposed, canopy-shaded, and artificially shaded) for three subsequent years. Variables in boldface are significant.

Taxonomic group	**Predictor**	**Df**	**Variance**	***F*-value**	***p*-value**
a) Saproxylic beetles (logs)	**Tree species**	**5**	**1.09 e^{-01}**	**4.60**	**0.001**
	Treatment	**2**	**8.84 e^{-02}**	**9.34**	**0.001**
	Space	**2**	**2.44 e^{-02}**	**2.57**	**0.001**
	Residual	98	4.64 e^{-01}		
b) Wood-inhabiting fungi (logs)	**Tree species**	**5**	**8.62 e^{-02}**	**2.78**	**0.001**
	Treatment	**2**	**2.20 e^{-02}**	**1.77**	**0.009**
	Space	**2**	**2.11 e^{-02}**	**1.70**	**0.017**
	Residual	98	6.08 e^{-01}		
c) Spiders (logs)	Tree species	5	2.18 e^{-02}	8.88 e^{-01}	0.706
	Treatment	**2**	**1.65 e^{-01}**	**16.78**	**0.001**
	Space	**2**	**5.27 e^{-02}**	**5.35**	**0.001**
	Residual	98	4.82 e^{-01}		
d) Saproxylic beetles (branches)	**Tree species**	**5**	**2.76 e^{-01}**	**4.49**	**0.001**
	Treatment	**2**	**5.31 e^{-02}**	**2.16**	**0.003**
	Space	10	1.45 e^{-01}	1.18	0.124
	Residual	28	3.45 e^{-01}		

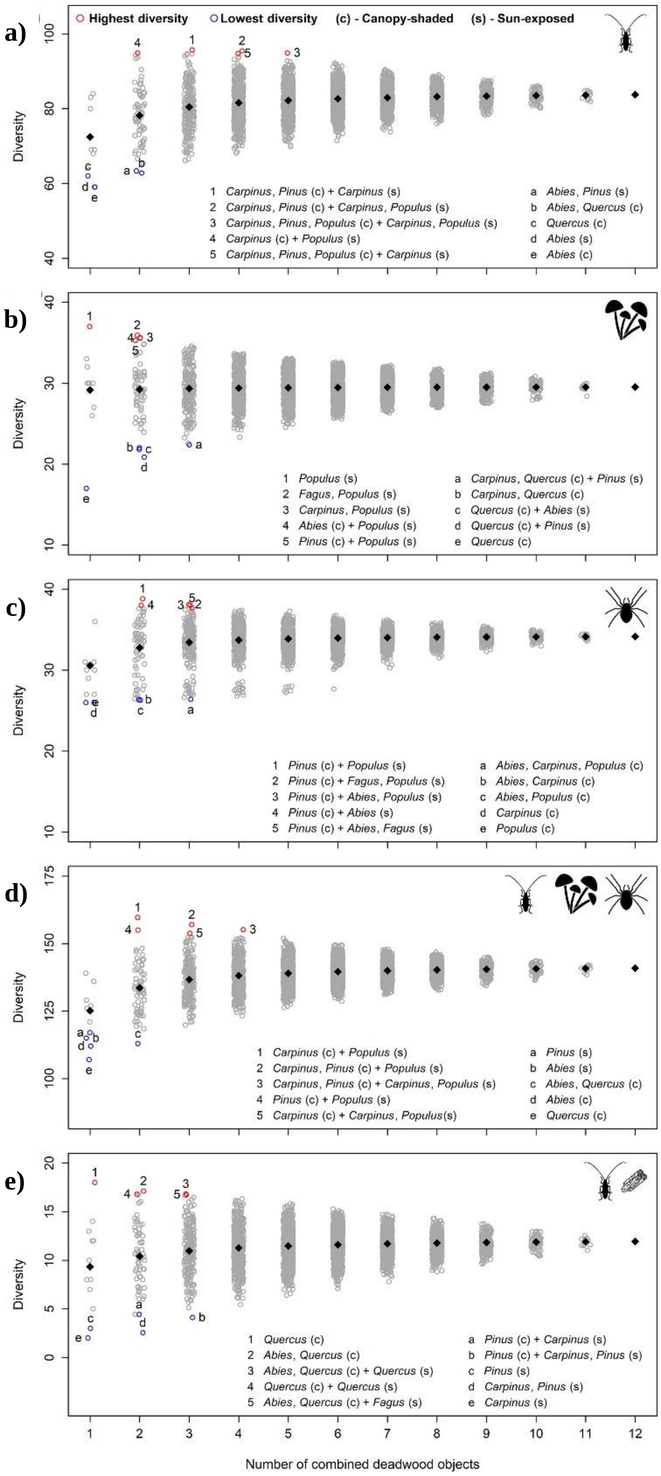

Figure II.4: The gamma-diversity (q = 0) of **a)** saproxylic beetles in logs, **b)** wood-inhabiting fungi in logs, **c)** spiders in logs, **d)** pooled taxa in logs and **e)** saproxylic beetles in branches for all possible combinations of the six tree species, either sun-exposed or canopy shaded, rarefied to six logs/branch bundles. The black diamonds indicate the means. The five combinations of tree species and sun exposure resulting in the lowest gamma-diversity are indicated by blue circles and black letters, and the five combinations resulting in the highest gamma-diversity by red circles and black numbers. (c) Represent canopy-shaded tree species, and (s) represent sun-exposed deadwood objects. For a full list of all combinations and the resulting gamma-diversity, see Tables S12–S16. Species were recorded in deadwood objects of six different tree species subjected to two different sun exposure treatments for three subsequent years.

II.5 Discussion

Our results showed a strong influence of sun exposure and tree species on the alpha- and beta-diversity of saproxylic communities. Divergent from our hypotheses, the effect of sun exposure was generally positive for all taxa recorded in logs, but negative for saproxylic beetles reared from branches. Tree species was of variable importance for taxa of saproxylic beetles and wood-inhabiting fungi. These results demonstrate the importance of considering tree species and the degree of sun exposures in integrative conservation strategies aimed at enhancing saproxylic biodiversity in European forests.

Effects of sun exposure

Sun exposure was the most important driver of alpha-diversity across all analysed taxa in logs and for the beta-diversity of saproxylic beetles and spiders, but not for the beta-diversity of wood-inhabiting fungi (Table II.1; see Supporting Information S2). Higher numbers of saproxylic beetle and spider species in sun-exposed logs were among the predictions of this study and consistent with earlier studies (Seibold *et al*., 2016b; Thorn *et al*., 2016a). Our results similarly showed that sun exposure was the most important driver of the beta-diversity of these groups (Table II.1). The preference of saproxylic beetles for sun-exposed deadwood was previously described (Seibold *et al*., 2015a, 2015b) and can perhaps be explained by the fact that greater sun exposure increases the body temperature and thus the metabolism of poikilothermic arthropods (Brown *et al*., 2004; Müller *et al*., 2015a). Spiders might also benefit from sun-exposed deadwood by the increase in their activity resulting from the higher temperatures and by the greater availability of potential prey. Contrasting to our hypothesis, the higher species numbers of wood-inhabiting fungi in sun-exposed logs was, however, surprising, as fungal species numbers were predicted to be higher in the artificially shaded or canopy-shaded logs, as both would have offered a higher humidity (Bässler *et al*., 2010b; Talley *et al*., 2002). However, the laboratory experiment of Venugopal *et al*. (2016) showed that fungal activity increases with increasing temperature and humidity. Hence, the higher temperatures in combination with higher humidity might be preferential and have interacted with the activity of wood-inhabiting fungi to promote their species diversity in response to the more rapidly decaying wood. Nonetheless, we detected no differences in fungal species numbers between sun-exposed and artificially shaded plots. In contrast to saproxylic beetles and spiders, sun exposure had lower impact on the beta-diversity of wood-inhabiting fungi than tree species (Table II.1). This finding indicates, that wood-inhabiting fungi do not underlie large dispersal limitations in our study area and that colonisation success of wood-inhabiting fungi is more likely to be determined by tree species than by the spatial distance between deadwood structures (Abrego *et al*., 2018; Krah *et al*., 2018).

The alpha- and beta-diversity of saproxylic beetles in branches was also influenced by sun exposure (Table II.1; see Supporting Information S2 and S4), but divergent from our hypothesis. In theory, sun exposure might have a much stronger effect on deadwood of small than of larger dimensions (Müller *et al*., 2015a). The less constant microclimatic conditions that occur within deadwood of small diameter increase the probability of humidity drainage, in turn challenging the survival and successful larval development of saproxylic beetles. This would explain the lower alpha-diversity of saproxylic beetles determined in our study (see Supporting Information S2). Indeed, saproxylic beetles in deadwood of small diameters benefited more from shaded than from sun-exposed conditions, as evidenced by the higher species numbers under artificially shaded and canopy-shaded conditions (see Supporting Information S2).

Effects of tree species

For saproxylic beetles in logs, species numbers were highest in *Carpinus* followed by *Populus* (Figure II.2). Gossner *et al*. (2016) similarly found that alpha-diversity was higher in *Carpinus* logs than in the logs of 12 other tree species, but it was lower in *Populus* logs, although only shaded conditions were investigated in that study. Both, *Carpinus* and *Populus* as softwood tree species undergo faster decay than, e.g. *Quercus* (Kahl *et al*., 2017), which might have resulted in a higher diversity of niches per log within the investigated time period and thus a higher species richness. Hardwood tree species with distinct heartwood, including *Quercus*, also tend to have a higher resistance to decomposers, as the concentrations of tree metabolites are often higher than in sapwood and more toxic (Noll *et al*., 2016). The lower species numbers of saproxylic beetles in *Abies* and *Pinus* are consistent with the production by coniferous tree species of larger amounts of primary and secondary metabolites that prevent colonisation (Kahl *et al*., 2017). Additionally, coniferous tree species have a higher lignin content, which also slows their decomposition (Weedon *et al*., 2009).

Divergent decay rates among tree species might also have been responsible for the differences in the species numbers of saproxylic beetles in logs and branches. The importance of branches, but not of logs from *Quercus* can be explained by the slower decay rate and thus the greater durability of logs compared to branches. This would extend the time available for the successful colonisation and development in deadwood of a larger number of species.

Similar to saproxylic beetles, wood-inhabiting fungi had the highest species numbers in logs of *Fagus*, *Carpinus*, and *Populus* (Figure II.2). This is partially in contrast to the results of a previous study (Purahong *et al.*, 2018b) in which higher numbers of fungal operational taxonomic units (OTUs) were found associated with logs of coniferous than of broadleaved trees in early decay, although no basidiomes were recorded and DNA of wood-inhabiting fungal species can be present without fructification. The colonisation and fructification of wood-inhabiting fungi are determined by certain characteristics of the host tree species (Purahong *et al.*, 2018c), the presence of other fungal species (Fukami *et al.*, 2010), and the amount of time elapsed after the death of the tree (Yuan *et al.*, 2017). Fungal species colonising coniferous tree species might fructify at a later time than those that colonise broadleaved tree species, as the larger amounts and longer persistence of metabolites of coniferous trees and the slower rate of decomposition of those species may inhibit fructification (Kahl *et al.*, 2017; Weedon *et al.*, 2009). Larger amounts of metabolites might also reduce the colonisation of living trees by endophytic wood-inhabiting fungi, which are inactive in the living tree and become active as it weakens or dies (Parfitt *et al.*, 2010).

Tree-species-specific effects of sun exposure

The alpha-diversity of single tree species across all investigated taxa followed the general positive trend determined for sun exposure (Figure II.3; see Supporting Information S2 and S4). However, a positive correlation between sun exposure and the species numbers of the studied taxa (Figure II.3) was identified only for shade-intolerant (*Quercus*, *Populus*, and *Pinus*), not for shade-tolerant (*Fagus*, *Carpinus*, and *Abies*) tree species. These findings suggest that shade-intolerant tree species and their associated communities are adapted to sun-exposed conditions whereas the opposite is the case for shade-tolerant tree species (Lindhe *et al.*, 2005; Müller *et al.*, 2015b). For instance, many saproxylic specialists on oak prefer sun-exposed deadwood (Ranius & Jansson, 2000). Our results are in line with those of Gossner *et al.* (2016), who also reported that the shade preference of tree species did not correlate with alpha-diversity; rather, there was only a general increase in species richness with increasing sun exposure. However, the experimental approach used in those studies was limited to a short canopy cover gradient ranging from 60 to 100 %. The lack of a high sun exposure condition in those studies might have masked potential correlations between the shade tolerance of the different tree species and the species richness of the studied organisms.

Effects of space on beta-diversity

An influence of spatial distance on beta-diversity was consistently observed, but only for the saproxylic taxa recorded in logs (Table II.1). Spatial distance serves as a proxy for several factors, including local stand characteristics, stand management type, the geology of the respective site, and the spatial arrangement of the deadwood (Baber *et al*., 2016; Gossner *et al*., 2016). Saproxylic species are limited in their dispersal abilities, which range from a few hundreds of meters to a few kilometers (saproxylic beetles) to tens of kilometers (wood-inhabiting fungi), although studies investigating long-distance dispersal are scarce (Komonen & Müller, 2018). For instance communities of wood-inhabiting fungi analysed by air sampling of spores showed no variation collected <10 km apart in their composition, but >100 km apart sites (Abrego *et al*., 2018). By contrast, spatial distance had no influence on saproxylic beetles reared from branches. Small-diameter deadwood is more frequent than deadwood of larger diameters and its resource patches are better connected. Moreover, smaller diameters might be colonised by smaller species and in general of larger populations (Bussler *et al*., 2011). Hence, saproxylic species colonising smaller-diameter deadwood are more equally distributed and do not have to overcome large distances to find new resources suitable for colonisation.

Combinations of tree species and sun exposure

Overall, the combinations of tree species and sun exposure that supported the highest diversity were composed of *Carpinus* and *Populus* together with branches of *Quercus* and coniferous trees and in part of other broadleaved tree species (see Supporting Information S12–S16). Those combinations likely merged the most complementary saproxylic communities, as demonstrated by Gossner *et al*. (2016) and Andringa *et al*. (2019) for combinations of tree species and of tree species and decay stages. Differences in the community composition of saproxylic taxa have been attributed to differences in sun exposure (Seibold *et al*., 2016a) and to the wood-related properties of single tree species (Purahong *et al*., 2018c). Hence, most of the effectual combinations of sun exposure and tree species seem to depend on the most complementary niches in deadwood.

II.6 Management implications

Beside the accumulation of deadwood by passive conservation measures, an active enrichment of deadwood has been promoted to accelerate habitat restoration. However, strategies of active deadwood enrichment in Central European managed forests mainly consist of enriching deadwood amounts at high economic efforts but disregard the recently identified higher importance of deadwood quality and diversity for biodiversity. Our study demonstrated that different tree species and particularly different degrees of sun exposure are needed to effectively promote biodiversity. We therefore recommend to create deadwood structures at sun-exposed forest edges or with the help of gap cuttings. Additionally, standing dead trees or natural disturbances, such as windthrows, can be used, as both naturally generate many different types of sun-exposed structures. Based on the six model tree species included in this study, we recommend prioritizing *Carpinus*, *Pinus*, *Populus*, and *Quercus* to achieve the highest diversity among the taxa analysed in this study. Generally, combinations of tree species should include hardwood and softwood broadleaved trees as well as coniferous tree species. Lastly, a landscape wide enrichment of deadwood should be considered to cover different local conditions and to increase the effectiveness of enrichment strategies based on deadwood.

II.7 Data availability

Analysed data are available in the Dryad Digital Repository: doi: 10.5061/dryad.rn8pk0p6n.

II.8 Acknowledgements

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II.9 Supporting Information

All Supporting Information are electronically attached and public available online.

Chapter III: Diversity and conservation of saproxylic beetles of 42 European tree species – an experimental approach from early successional stages using branches

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III.1 Abstract

(1) Tree species diversity is important to maintain saproxylic beetle diversity in managed forests. However, knowledge about the conservational importance of single tree species and implications for forest management and conservation practices are lacking.

(2) We exposed freshly cut branch-bundles of 42 tree species, representing tree species native and non-native to Europe, under sun-exposed and shaded conditions for one year. Afterwards, communities of saproxylic beetles were reared ex-situ for two years. We tested for the impact of tree species and sun exposure on alpha-, beta-, and gamma-diversity as well as composition of saproxylic beetle communities. Furthermore, the number of colonised tree species by each saproxylic beetle species was determined.

(3) Tree species had a lower impact on saproxylic beetle communities compared to sun exposure. The diversity of saproxylic beetles varied strongly among tree species, with highest alpha- and gamma-diversity found in *Quercus petraea*. Red-listed saproxylic beetle species occurred ubiquitously among tree species. We found distinct differences in the community composition of broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood.

(4) Our study enhances the understanding of the importance of previously understudied and non-native tree species for the diversity of saproxylic beetles. To improve conservation practices for saproxylic beetles and especially red-listed species, we suggest a stronger incorporation of tree species diversity and sun exposure into forest management strategies,

including the enrichment of deadwood from native and with a specific focus on locally rare or silvicultural less important tree species.

III.2 Introduction

Human impacts have modified forest ecosystems worldwide (Newbold *et al.*, 2015). Intensive logging, altered disturbance regimes, and changes in forest structure have resulted in massive declines of ecological key elements, particularly in Europe (Lindenmayer *et al.*, 2008; Lindenmayer *et al.*, 2012b; Thorn *et al.*, 2020). For centuries, dead and moribund trees have been extracted, as they were considered to be a waste of resources and to serve as a hatchery of forest pathogens (Cotta, 1865; Grove, 2002). Moreover, forest management practices have decreased the diversity of native tree species, for instance by the establishment of coniferous tree plantations (Schelhaas *et al.*, 2003) and the parallel introduction of various non-native tree species (Richardson & Rejmánek, 2011; Savill, 2015).

Deadwood plays an important role in nutrient cycles in addition to providing multiple ecosystem functions, including carbon storage (Lindenmayer *et al.*, 2014). In Europe, approximately one-quarter of all forest-dwelling species depend on deadwood (Siitonen, 2001). These saproxylic species are highly sensitive to changes in deadwood abundance and diversity (Seibold *et al.*, 2016b; Ulyshen & Hanula, 2009), and many saproxylic species have therefore suffered following deadwood removal as a result of forest management (Seibold *et al.*, 2015b; Speight, 1989). Yet, 20–30 % of all European saproxylic beetle species are red-listed (Cálix *et al.*, 2018; Seibold *et al.*, 2015b).

Habitat suitability for saproxylic beetles is determined by multiple extrinsic and intrinsic factors (reviewed in Seibold *et al.*, 2015a; Müller *et al.*, 2020). Besides the amount of deadwood, most important are the deadwood type (e.g. stump/log/branch), the position (laying/standing) (Ulyshen & Hanula, 2009), the diameter (Buse *et al.*, 2008; Kostanjsek *et al.*, 2018), the decay stage (Parisi *et al.*, 2018), local stand characteristics (Müller *et al.*, 2015b), and particular microclimate related to sun exposure (Müller *et al.*, 2015a; Müller *et al.*, 2020; Thorn *et al.*, 2016a). Another substantial factor for saproxylic beetles is the identity of their respective host tree species (Müller *et al.*, 2020; Vogel *et al.*, 2020). Saproxylic beetle species can be largely polyphagous, colonising a variety of different tree species, up to monophagous species, which are restricted to a single host tree species (Milberg *et al.*, 2014; Toivanen & Kotiaho, 2010), while a clear distinction between broadleaved and coniferous tree species exists (Vogel *et al.*, 2020). The host specificity of saproxylic beetles extenuates over the course of the decay process and seems to be higher in species directly feeding on deadwood compared to predatory species (Wende *et al*., 2017). However, investigations of the host tree specificity of saproxylic beetles have mostly been based on occasional observations or field surveys (e.g. Palm, 1959; Hellrigl, 1978a, 1978b; Bense, 1995; Klausnitzer *et al*., 2015) whereas experimental approaches (e.g. rearing or exclusion studies) under standardized conditions are scarce and regularly involve only a small subset of available tree species (e.g. Lindhe & Lindelöw, 2004; Brin *et al*., 2011; Müller *et al*., 2015b; Andringa *et al*., 2019), limiting generalised statements regarding host tree specificity. Moreover, several approaches tried to examine the conservational importance of single tree species for saproxylic beetles (Andringa *et al*., 2019; Jonsell *et al*., 1998; Müller *et al*., 2015b). In Europe, common oak (*Quercus robur*) is regarded as the most species-rich tree species, in addition to hosting the highest diversity of red-listed saproxylic beetles (Brändle & Brandl, 2001; Jonsell *et al*., 1998). Comprehensive recommendations about tree species and the combinations thereof that effectively support the highest diversities of saproxylic beetles are provided in the studies of Vogel *et al*. (2020), Gossner *et al*. (2016), and Andringa *et al*. (2019), in which 6, 13, and 20 tree species are compared. Those studies identified high diversities of saproxylic beetles, particularly in relation to hornbeam (*Carpinus betulus*), poplar (*Populus* sp.), and Norway spruce (*Picea abies*) as well as combinations of these tree species, including those of broadleaved and coniferous tree species.

Within the past two decades there has been increasing recognition of the importance of deadwood for conservation (reviewed in Vítková *et al*., 2018). Conservation strategies have thus been developed by incorporating an active enrichment of deadwood during logging operations, but their focus is the amount of deadwood from regionally dominant tree species, such as European beech (*Fagus sylvatica*), whereas other aspects of deadwood quality have been largely neglected. Furthermore, single tree species, such as *P. abies* and oak (*Quercus* sp.), are commonly excluded from deadwood enrichment, whether by policy or for reasons of forest protection (Alexander, 2016; Brown *et al*., 2015; Gößwein *et al*., 2017). Consequently, both silvicultural unimportant and rare tree species, such as hawthorn (*Crataegus* sp.) and checker tree (*Sorbus torminalis*), have been largely ignored. Furthermore, little is known about the importance of tree species non-native to Central Europe for saproxylic beetles, such as Douglas fir (*Pseudotsuga menziesii*) and sweet chestnut (*Castanea sativa*), although the increased cultivation and introduction of these trees have been discussed with respect to climate change and other purposes (Bolte *et al*., 2009; Richardson & Rejmánek, 2011; Schmid *et al*., 2014).

Here, we expanded the list of tree species experimentally sampled for saproxylic beetles by investigating 42 different broadleaved and coniferous tree species. These tree species represent > 50 % of all native tree species distributed in Central Europe and also include the most important non-native tree species of silvicultural interest, covering essential parts of taxonomic and phylogenetic diversity as well as proportions of forest cover (Rivers *et al.*, 2019; San-Miguel-Ayanz *et al.*, 2016). In our study, freshly cut branch-bundles were exposed for one season under two different conditions of sun exposure and their communities of saproxylic beetles afterwards reared ex situ. We quantified the impact of tree species and sun exposure on alpha-, beta-, and gamma-diversity as well as community composition of saproxylic beetles. Furthermore, the number of colonised host tree species of each species of saproxylic beetles was determined and compared between different larval feeding types.

III.3 Materials and methods

Study area and experimental design

Our study was conducted near the city of Bad Windsheim in north-western Bavaria, Germany (49°32' N 10°23' E) (Figure III.1a). In this area, the mean annual temperatures obtain around 9.2 °C and the mean annual precipitation 595 mm (Agrarmeteorologie Bayern, 2020). Forest stands in the study area are mainly composed by sessile oak (*Quercus petraea*) with lower percentages of *F. sylvatica*, Scots pine (*Pinus sylvestris*), and *P. abies* as well as a high variety of around 60 other tree species. Beside high-stem forests, the study area is partly managed as coppice with standards, thus promoting sun-exposed forest structures and *Q. petraea*. Overall, there are an estimated 500 species of saproxylic beetles in the study area (Bussler *et al.*, 2018).

The study was initiated in March 2017 by assembling 252 freshly cut branch-bundles from 42 different tree species on three plots (Figure III.1a). Each plot was divided into a sun-exposed subplot on a freshly logged area and a shaded subplot within the forest stand to capture the range of microclimate conditions. The distance between subplots was less than 100 m. The tree species were determined by Sebastian Vogel and Sven Finnberg according to Jäger *et al.* (2017). Tree species included 32 that are native to Central Europe: silver fir (*Abies alba*), field maple (*Acer campestre*), Norway maple (*Acer platanoides*), sycamore maple (*Acer pseudoplatanus*), black alder (*Alnus glutinosa*), grey alder (*Alnus incana*), birch (*Betula pendula*), *C. betulus*, common hazel (*Corylus avellana*), common hawthorn (*Crataegus monogyna*), *F. sylvatica*, alder buckthorn (*Frangula alnus*), European ash (*Fraxinus excelsior*), common juniper (*Juniperus communis*), European larch (*Larix decidua*), apple (*Malus domestica*), *P. abies*, *P. sylvestris*, aspen (*Populus tremula*), wild cherry (*Prunus avium*), blackthorn (*Prunus spinosa*), European wild pear (*Pyrus pyraster*), *Q. petraea*, goat willow (*Salix caprea*), black elder (*Sambucus nigra*), rowan (*Sorbus aucuparia*), service tree (*Sorbus domestica*), *S. torminalis*, yew (*Taxus baccata*), small-leaved lime (*Tilia cordata*), fluttering elm (*Ulmus laevis*), and field elm (*Ulmus minor*), and ten tree species non-native to Central Europe: grand fir (*Abies grandis*), Weymouth pine (*Pinus strobus*), black cherry (*Prunus serotina*), *P. menziesii*, northern red oak (*Quercus rubra*), and black locust (*Robinia pseudoacacia*) from North America. Also included were four species native to Southern Europe: *C. sativa*, common walnut (*Juglans regia*), black pine (*Pinus nigra*), and Turkey oak (*Quercus cerris*). On each subplot, a branch-bundle of every tree species was established, consisting of three branches each with a length of 100.6 (± 3.5) cm and a diameter of 4.9 (± 0.9) cm. Branch-bundles of four different tree species were randomly combined and then suspended from a metal pile, where they were left from March 2017 to February 2018 (Figure III.1b).

Between March 2018 and September 2019, beetles from the branch-bundles were reared in plastic tubes with trapping bottles attached (Figure III.1c). They were trapped with ethanol and identified by Heinz Bussler to the species level according to Freude *et al*. (1963–1984). The classification of beetles as saproxylic was based on the approach of Schmidl and Bussler (2004). Red List Categories were retrieved from the Bavarian Red List (StMUGV, 2005) and information on the larval feeding type of individual species (detritivorous, mycetophagous, xylophagous, zoophagous) from the study by Seibold *et al*. (2015b).

Figure III.1: The study area and experimental design. The study was conducted **a)** near the city of Bad Windsheim in north-western Bavaria (Germany), at three different sites (A-C). Each site consisted of two subplots: sun-exposed on a freshly logged area and canopy-shaded by the forest stand. The forest classification is based on Corine land cover data (version 20b2). **b)** On each subplot, a branch-bundle of every tree species was established. Branch-bundles from four tree species were randomly combined and suspended from metal piles from March 2017 to February 2018. **c)** Saproxylic beetles from the branch-bundles were reared in plastic tubes with attached trapping bottles from March 2018 until September 2019.

Data analysis

All analyses were performed using R 3.6.2 (R Development Core Team, 2019b). To quantify the relative impact of tree species and sun exposure on beta-diversity of saproxylic beetles, we applied a regularized discriminant analysis (RDA; Friedman, 1989). For the RDA, we generated distance matrices by the function dist´ (package `proxy´; Meyer & Buchta, 2019) , in detail a cophenetic distance based on the phylogenetic tree of European flora provided by Durka and Michalski (2012), as a proxy of distances between different tree species as well as a spatial distance between subplots based on the distance-based Moran`s eigenvector map (Dray *et al*., 2006). Distances in species composition of saproxylic beetles were calculated based on Hellinger transformed species data. Within the RDA, sun exposure (sun-exposed/shaded) was used as a factor. The RDA was followed by a subsequent analysis of variance by the function `ANOVA´ (package `vegan´; Oksanen *et al*., 2019).

The alpha-diversity of tree species was ranked by applying a generalised linear mixed-effects model with a Poisson error distribution (package `lme4´; Bates *et al*., 2015). In addition to the tree species, the model included the branch volume as a predictor to control for variations in branch diameter and resource amount (Müller *et al*., 2015a) as well as the plot identity as a random effect to account for replicated measurements at the plot level (for model equations see Supporting Information S2). Differences in in species diversity between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood were quantified via a separate generalised linear mixed-effects model using the branch volume as an additional predictor and the plot identity and tree species as random effects (see Supporting Information S2).

The observed gamma-diversity of the tree species was ranked based on the total number of observed and red-listed saproxylic beetle species per tree species. The estimated gamma-diversity between tree species, broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood was determined by estimating the species richness (sensu Gotelli & Colwell, 2001) using sample-based rarefaction-extrapolation curves (package `iNEXT´; Chao *et al*., 2014; Hsieh *et al*., 2016).

Differences in communities were visualized by nonmetric multidimensional scaling (NMDS; package `vegan´; Oksanen *et al.,* 2019). The distance to the NMDS centroid of broadleaved and coniferous tree species served as a measure of uniqueness for each host tree species in terms of saproxylic beetle communities (Villéger *et al*., 2010). To compare communities between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood, we applied a permutational analysis of variance using distance matrices with branch volume as an additional predictor by the function \`adonis2´ (package \`vegan´; Oksanen *et al*., 2019). The plot identity was used as strata to constrain permutations.

The number of colonised tree species between different larval feeding types was compared by using a linear model (package \`stats´; R Development Core Team, 2019b) and a linear inference procedure with simultaneous adjustment of *p*-values by means of the function \`glht´ (package \`mulltcomp´; Hothorn *et al*., 2008).

III.4 Results

Overall, 113 species of saproxylic beetles with a total of 30,550 individuals were reared, including 20 red-listed species (for a detailed list of the recorded species see Supporting Information S1). This species number corresponds to 20 % of all saproxylic beetles recorded in the study area. The recorded species belonged to 23 different families, with highest abundances and species numbers attributed to Curculionidae (26,242 individuals/28 species, including Scolytinae), Cerambycidae (2,069/29), and Buprestidae (1,285/9).

Tree species had a lower impact on saproxylic beetle communities compared to sun exposure (Table III.1). The highest alpha-diversity occurred among saproxylic beetles reared from *Q. petraea*, *Q. cerris* as well as *M. domestica*, and the lowest alpha-diversity among communities of saproxylic beetles was reared from *J. communis*, *U. laevis*, and *T. baccata* (Figure III.2a; see Supporting Information S3). The alpha-diversities of tree species correlated positively with the observed gamma-diversity (adjusted $R^2 = 0.84$, $p < 0.001$) (see Supporting Information S6a). Between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood the alpha-diversity of saproxylic beetles was similar (see Supporting Information S4).

Among broadleaved tree species, the highest observed gamma-diversity of saproxylic beetles was found in *Q. cerris*/*Q. petraea* (26 species), *M. domestica* (24), and *R. pseudoacacia* (18) as well as among coniferous tree species in *P. nigra* (22), *P. abies* (21), and *P. menziesii*/*P. strobus* (19) (Figure III.2b; see Supporting Information S1). The lowest observed gamma-diversity was found in association with *F. excelsio*r/*P. tremula*/*P. spinosa* (7), *F. alnus* (6), and *U. laevis* (3) as well as *A. alba* (8), *J. communis* (5), and *T. baccata* (3). Only *Q. rubra* (16) as a non-native tree species had a lower observed gamma-diversity than included native species from the same genus (*Q. petraea*). Species numbers were higher among saproxylic beetle communities reared form non-native *P. serotina* (13) compared to native *P. avium* (11) and *P. spinosa* as well as from non-native *P. nigra, P. strobus,* and *A. grandis* (10) than from native

P. sylvestris (18) and *A. alba*. Even non-native tree species such as *P. menziesii* and *R. pseudoacacia* had a higher observed gamma-diversity than several native tree species. Among red-listed species, the highest species numbers were found in *Q. cerris* (5), *M. domestica*/*T. cordata* (4), and *A. grandis*/*A. glutinosa*/*C. betulus*/*Q. petraea*/*S. aucuparia*/*S. caprea* (3) (Figure III.2b). For all tree species, the number of red-listed saproxylic beetle species increased as the total number of observed species increased (adjusted $R^2 = 0.23$, $p = 0.002$) (Supporting Information S6b). The estimated and observed gamma-diversity slightly differed (Figure III.2b, c), with the highest estimated gamma-diversity among saproxylic beetle communities reared from *Q. petraea*, *P. abies*, and *R. pseudoacacia*, and the lowest estimated gamma-diversity among those from *J. communis*, *U. laevis*, and *T. baccata*. The estimated gamma-diversity of saproxylic beetles was higher in broadleaved compared to coniferous but comparable between native and non-native tree species, while no differences were found between sun-exposed and shaded deadwood (see Supporting Information S5).

Table III.1: Effects of tree species, sun exposure, and spatial distribution on the beta-diversity of saproxylic beetle communities. Results based on a regularized discriminant analysis (RDA). Variables in boldface are significant.

Predictor	Df	Variance	*F*-value	*p*-value
Tree species	**41**	**2.86 e−01**	**2.82**	**< 0.001**
Sun exposure	**1**	**9.41 e−03**	**3.80**	**< 0.001**
Spatial distribution	**1**	**3.89 e−03**	**1.57**	**0.045**
Residual	208	5.15 e−01		

Communities of saproxylic beetles in broadleaved and coniferous tree species were distinctly different (Figure III.3; see Supporting Information S7). The most unique community compositions for broadleaved and coniferous tree species were those occurring in association with *U. laevis*, *F. alnus*, and *J. communis* (Figure III.2d). Communities of saproxylic beetles also differed between native and non-native tree species as well as between sun-exposed and shaded deadwood (Supporting Information S7).

In our study, 37 saproxylic beetle species were exclusively found in a single tree species (see Supporting Information S1). Overall, saproxylic beetle species colonised a mean of 4.89 host tree species, with the highest number colonised by *Litargus connexus* (41 tree species). Red-listed saproxylic beetle species colonised a mean of 2.95 host tree species (see Supporting Information S1) but did not necessarily have a higher host tree specificity, although the number of colonised tree species increased with the increasing abundance of single species of saproxylic beetles (adjusted $R^2 = 0.35$, $p < 0.001$) (see Supporting Information S8). Mycethophagous beetle species colonised significantly higher number of tree species compared to detritivorous, xylophagous and zoophagous beetle species (see Supporting Information S9).

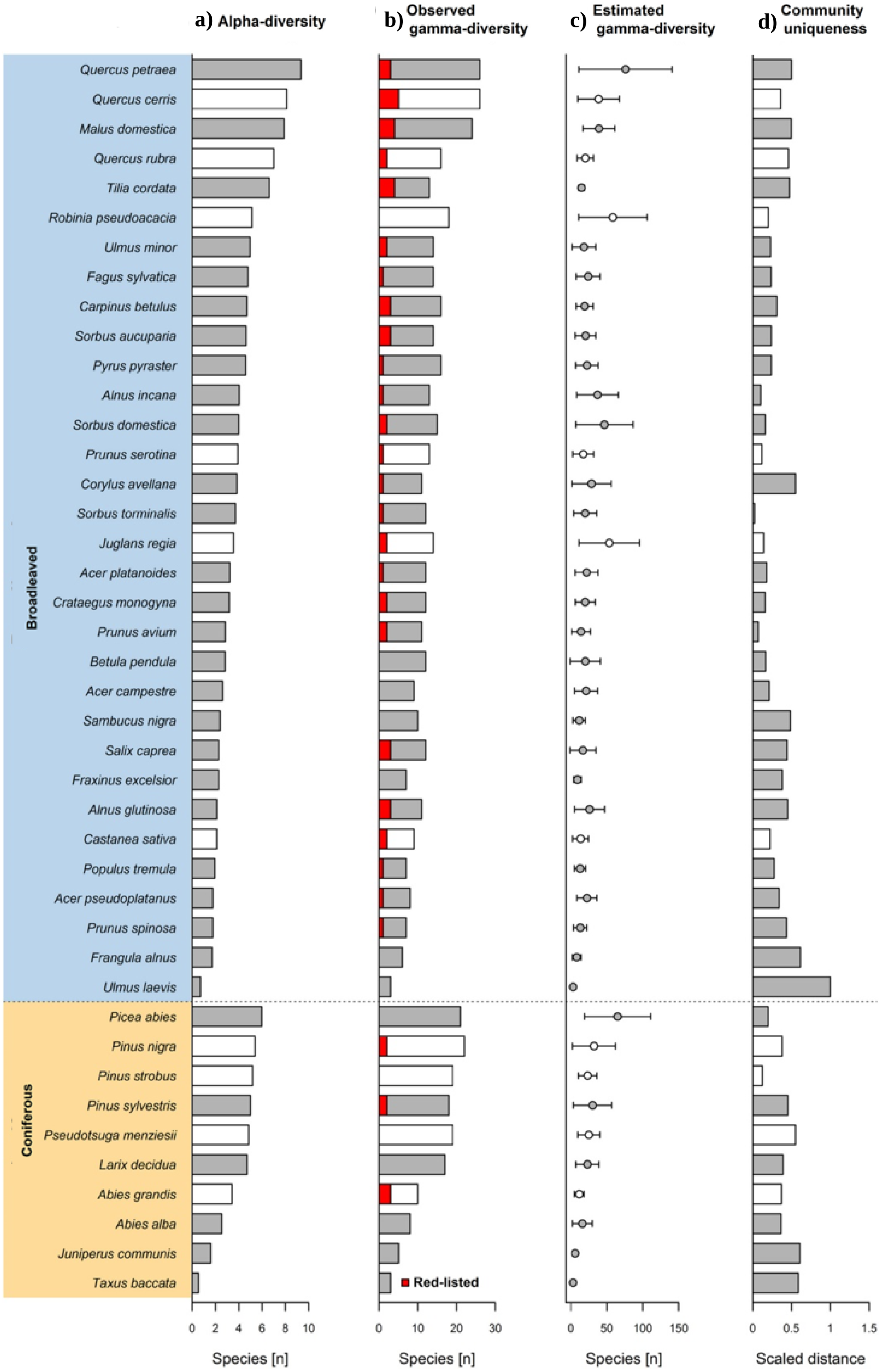

Figure III.2: a) Alpha-diversity estimated by a generalised linear mixed-effects model with species richness as response and tree species as well as branch volume as predictors, **b)** observed gamma-diversity and number of red-listed species, **c)** estimated gamma-diversity, and **d)** uniqueness of the saproxylic beetle communities among tree species, measured as mean distance to the NMDS centroid of all broadleaved respective coniferous tree species. Native tree species are represented by grey bars, non-native tree species by white bars.

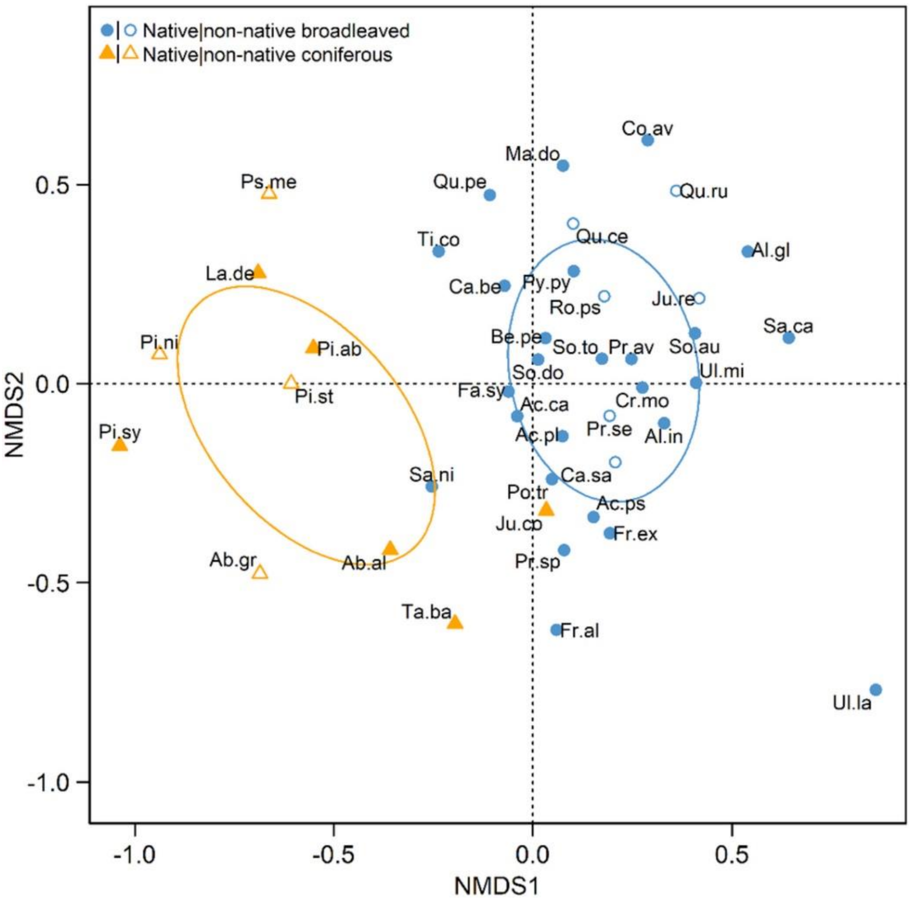

Figure III.3: Nonmetric multidimensional scaling of the saproxylic beetle communities found in different tree species: Ab.al = *Abies alba*, Ab.gr = *Abies grandis*, Ac.ca = *Acer campestre*, Ac.pl = *Acer platanoides*, Ac.ps = *Acer pseudoplatanus*, Al.gl = *Alnus glutinosa*, Al.in = *Alnus incana*, Be.pe = *Betula pendula*, Ca.be = *Carpinus betulus*, Ca.sa = *Castanea sativa*, Co.av = *Corylus avellana*, Cr.mo = *Crataegus monogyna*, Fa.sy = *Fagus sylvatica*, Fr.al = *Frangula alnus*, Fr.ex = *Fraxinus excelsior*, Ju.co = *Juniperus communis*, Ju.re = *Juglans regia*, La.de = *Larix decidua*, Ma.do = *Malus domestica*, Pi.ab = *Picea abies*, Pi.ni = *Pinus nigra*, Pi.st = *Pinus strobus*, Pi.sy = *Pinus sylvestris*, Po.tr = *Populus tremula*, Pr.av = *Prunus avium*, Pr.se = *Prunus serotina*, Pr.sp = *Prunus spinosa*, Ps.me = *Pseudotsuga menziesii*, Py.py = *Pyrus pyraster*, Qu.ce = *Quercus cerris*, Qu.pe = *Quercus petraea*, Qu.ru = *Quercus rubra*, Ro.ps = *Robinia pseudoacacia*, Sa.ca = *Salix caprea*, Sa.ni = *Sambucus nigra*, So.au = *Sorbus aucuparia*, So.do = *Sorbus domestica*, So.to = *Sorbus torminalis*, Ta.ba = *Taxus baccata*, Ti.co = *Tilia cordata*, Ul.la = *Ulmus laevis*, Ul.mi = *Ulmus minor*.

III.5 Discussion

Even if the tree species was of less importance compared to sun exposure, it had a significant impact on communities of saproxylic beetles. In our study, a few dominant tree species hosted the majority of saproxylic beetle diversity, but tree species with a medium or low overall diversity were of high importance for red-listed beetle species as well. Non-native tree species revealed no lower estimated gamma-diversity of saproxylic beetles compared to native tree species. Community composition largely differed between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood. Moreover, our results provide the first insights into the host tree specificity of single saproxylic beetle species by comparing a large number of tree species within one experimental approach.

Impact of sun exposure

Sun exposure revealed a higher relative impact on beta-diversity of saproxylic beetle communities than tree species, whereby no differences in alpha-diversity and estimated gamma-diversity were found (Supporting Information S4 and S5c). Nonetheless, community composition of saproxylic beetles varied distinctly between sun-exposed and shaded deadwood. Hence, our findings are partially in line to other studies of saproxylic beetles in branches, such as by Vogel *et al*. (2020) or Hardersen *et al*. (2020). The study of Vogel *et al*. (2020) revealed a higher impact of tree species on the beta-diversity of saproxylic beetle in branches, but of sun exposure in logs. Furthermore, the alpha-diversity of saproxylic beetles in Vogel *et al*. (2020) was higher in shaded compared to sun-exposed branches, what could not be supported by the present study. The lower alpha-diversity of saproxylic beetles in sun-exposed branches was possibly caused by a reduced buffering towards extreme microclimatic conditions (i.e. heat and drought) in comparison to logs, challenging the survival and successful larval development of saproxylic beetles.

Ranking of tree species

The alpha- and observed gamma-diversity of host tree species varied distinctly between different tree species (Figure III.2a, b) but were positively correlated to each other (see Supporting Information S6a). Overall, the highest alpha-, observed, and estimated gamma-diversity occurred in *Q. petraea* (Figs. III.2 and III.3), confirming the high importance of this tree species for saproxylic beetles (Brändle & Brandl, 2001). At least for the early decay stage, our finding is in line with other studies based on branches (Jonsell *et al*., 2007; Vogel *et al*., 2020), whereas in studies of logs the diversity in *Quercus* sp. was lower than in *C. betulus* or *P. tremula*, probably due to the faster decay rate of these tree species compared to *Quercus* sp. (Gossner *et al*., 2016), having an adverse effect in branches. The 38 saproxylic beetle species and particular 7 red-listed species recorded in *Q. petraea, Q. cerris,* and *Q. rubra* (34 % of 113 species; 35 % of 20 red-listed species) corresponded to the approximately 30 % of all red-listed species colonising *Quercus* sp. in Sweden (Jonsell *et al*., 1998). Nevertheless, the importance of *Quercus* sp. for saproxylic beetles is also related to other features, such as the age and diameter of the tree species as well as the probability for containing microhabitats (Paillet *et al*., 2019), none of which were considered in our study. Hence, the relevance of *Quercus* sp. for saproxylic beetles might reflect the dominance of this tree genus in the study area, as it would then generate the highest amount and diversity of deadwood. A preference of saproxylic beetles for the dominant tree species was also reported by Brändle & Brandl (2001) and by Bussler *et al*. (2011) based on databases of host tree species and their associated saproxylic beetles. Yet, this assumption was not applicable to the high diversity in *M. domestica*, as this tree species is artificially planted in the study area and its closest relative, the European crab apple (*Malus sylvestris*), is only marginally available. The high diversity of saproxylic beetles in *Pinus* sp., *P. abies*, *P. menziesii*, and *L. decidua* was unexpected as well (Figure III.2a–c) because these coniferous tree species are naturally rare in the study area or have been planted in small numbers. Saint-Germain *et al*. (2007) noted that coniferous tree species in early decay stages host higher species numbers of saproxylic beetles than broadleaved tree species, whose diversity typically increases during middle or later decay stages. Thus, the high alpha- and observed gamma-diversity found in coniferous tree species may have been due to the early decay stages of the branches included in our study. By contrast, the diversity of saproxylic beetles found in *F. sylvatica* was lower than expected, although this tree species has been reported to host a diversity of saproxylic beetles that is roughly the highest after *Quercus* sp. (Walentowski *et al*., 2014).

The tree species with the lowest alpha-diversity in our study were also those with the lowest observed and estimated gamma-diversity: *J. communis*, *U. laevis*, and *T. baccata* (Figure III.2a–c). This pattern was somewhat surprising, given that *U. minor*, for instance, had a distinctly higher diversity than *U. laevis* and the diversity of most of the other coniferous tree species was distinctly higher than that of *J. communis* and *T. baccata*. For all three tree species, the reduced diversity may reflect their different defence mechanisms. In several tree species, primary and secondary metabolites, such as oils, waxes, resins, tannins, terpenes, and polyphenols, have been shown to prevent wood colonisation by saproxylic insects (Erbilgin, 2019; Noll *et al*., 2016; Pearce, 1996). *U. laevis* contains higher amounts of terpenes than *U. minor* and is therefore more resistant against elm bark beetle (*Scolytus scolytus*) and elm dieback (Martín *et al*., 2004; Pajares *et al*., 2004). In the case of *J. communis*, resin can act as an impediment, and nearly all parts of *T. baccata* contain toxic taxanes. The distinct heartwood of *J. communis* and *T. baccata* may also confer a higher general resistance against decomposers, since its concentrations of metabolites are often higher and more toxic than those of sapwood (Kahl *et al*., 2017; Moll *et al*., 2018). Moreover, the degradation of defence mechanisms can allow a reduced host tree specificity of saproxylic beetles with increasing deadwood decomposition (Wende *et al*., 2017). Accordingly, beetle species of early succession, such as analysed in our study, will have a higher host tree specificity than beetle species of later decay stages (Parisi *et al*., 2018).

The number of red-listed species marginally increased with the increasing number of saproxylic species (see Supporting Information S6b), and some of the highest numbers of red-listed species were found in tree species with an overall high diversity (Figure III.2b). Yet, numerous red-listed species were hosted by tree species with only a low or medium alpha- and gamma-diversity, including *A. glutinosa*, *C. betulus*, *S. caprea*, *S. domestica*, and *T. cordata* (Figure III.2b; see Supporting Information S1). Together with the overall diversity of saproxylic beetles, this finding illustrates the importance of rare or silviculturally less important tree species for the diversity of saproxylic beetles (see also Andringa *et al*., 2019; Gossner *et al*., 2016; Vogel *et al*., 2020). Moreover, broadleaved tree species hosted most of the red-listed saproxylic beetles, in contrast to only three coniferous tree species (*P. nigra*, *P. sylvestris*, and *A. grandis*). In addition to the smaller number of coniferous tree species in the study area, this result may reflect the generally higher extinction risk of saproxylic beetles colonising broadleaved rather than coniferous tree species (Seibold *et al*., 2015b).

Non-native tree species

In our study, the alpha-diversity and estimated gamma-diversity between native and non-native tree species were similar, whereas the community composition varied significantly (see Supporting Information S4, S5b, and S7). Hence, our results are partially in line to those of other studies (Müller *et al*., 2015b; Ulyshen *et al*., 2018), whereby the importance of non-native tree species is still under debate with mixed scientific evidence. In the studies of Müller *et al*. (2015b) and Ulyshen *et al*. (2018), the species diversity associated with *P. menziesii* was significantly lower than that determined from native coniferous trees. Although in the studies of Bertheau *et al*. (2009) and Della Rocca *et al*. (2016), which included *P. menziesii* and *R.*

pseudoacacia, there were no differences in the species diversity of native versus non-native tree species. Andringa *et al*. (2019) also observed comparably high species respective family numbers in non-native *Larix kaempferi* and *Populus* x *canadensis*.

For red-listed beetle species, six of the nine non-native tree species were also accepted as host tree species. The three exceptions were *P. strobus, P. menziesii*, and *R. pseudoacacia*. Those tree species as well as *A. grandis* and *Q. rubra* were introduced into Central Europe from North America within the last 200 years (San-Miguel-Ayanz *et al*., 2016; Schmid *et al*., 2014), but adaption to novel tree species by saproxylic beetle specialists within this short time is unlikely (Gossner *et al*., 2009; Oleksa & Klejdysz, 2017). Generally, it is assumed that non-native tree species host more saproxylic beetle generalists than specialists (Ulyshen *et al*., 2018). Nevertheless, the presence of native congeneric tree species increases this process of adaptation (Branco *et al*., 2015; Pearse & Hipp, 2009), which would explain our finding of the relatively high species numbers of red-listed species in *A. grandis* and *Q. rubra* and the absence of red-listed species in *P. menziesii* and *R. pseudoacacia*, which have no European relatives. Additionally, the adaptation to non-native tree species might be promoted by a low geographical separation or an overlapping distribution of host trees and saproxylic beetle species, as is the case for *C. sativa*, *J. regia*, *P. nigra*, and *Q. cerris* from Southern Europe.

Determinants of host tree specificity

In our study, communities of saproxylic beetles distinctly differed between coniferous and broadleaved tree species but also within both groups of tree species (Figure III.3; see Supporting Information S7). This finding could indicate that factors beyond tree chemical defence mechanism determine saproxylic beetle communities. A possible explanation might be that the anatomical and physicochemical properties of deadwood strongly differ between broadleaved and coniferous tree species (Meerts, 2002; Weedon *et al*., 2009; Wilson & White, 1986), which can explain their frequently distinct communities of saproxylic taxa (Purahong *et al*., 2018c). Analyses of wood-inhabiting fungi and bacteria using molecular data and a small set of wood properties demonstrated the importance of physicochemical properties (pH, density, extractives, lignin content, and water content) in determining community composition (Moll *et al*., 2018; Purahong *et al*., 2018c). Additionally, the phylogenetic relatedness of the tree species might also play a role in determining saproxylic beetle communities, as wood properties seem to be more similar in closely related than in distantly related tree species (Purahong *et al*., 2018c; Thorn *et al*., 2015). This might further explain the differences between broadleaved and coniferous tree species as well as the differences between *J. communis*/*T. baccata*

(Cupressaceae/Taxaceae) and most other coniferous tree species (Pinaceae). Nevertheless, evidence supporting these assumptions should be the target of future studies including a larger number of tree species and information about their physicochemical/anatomical properties.

III.6 Management implications

Our study highlights the importance of previously understudied tree species and tree species that may become prospectively important due to climate change. Recent strategies on deadwood enrichment focus mainly on the amount of deadwood, whereas tree species diversity is of relatively low priority. Nonetheless, our study demonstrates the essential contribution of various tree species in maintaining saproxylic beetle diversity. Although branches represent only one type of deadwood, they are the most common type during active deadwood enrichment and can thus be considered as representative. Based on our results, we generally suggest a stronger incorporation of tree species diversity into conservation efforts targeting saproxylic beetles by considering the entirety of local tree species. This can be realised by the creation of sun-exposed forest structures and forest gaps in mainly closed forests, which are beneficial for the sun-preferring tree species (e.g. *S. caprea*, *S. nigra*, *J. communis*) and also for a variety of forest-dwelling species (Thorn *et al*., 2016a). Softwood and tree species of low economic value, for example *B. pendula* and *P. tremula*, should be allowed to undergo natural senescence and decay without intervention by forest management, as these short-living species provide a high diversity of ecological niches in deadwood and in early successional stages as well as following forest disturbances (Swanson *et al*., 2011; Thorn *et al*., 2020). Moreover, we recommend the promotion of naturally rare tree species to increase the local tree species diversity, while non-native tree species are rather unsuitable.

III.7 Data availability

Analysed data are available in the Dryad Digital Repository: doi: 10.5061/dryad.5x69p8d1b.

III.8 Acknowledgements

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III.9 Supporting Information

All Supporting Information are electronically attached and public available online.

Chapter IV: Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood

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IV.1 Abstract

Most parasites and parasitoids are adapted to overcome defense mechanisms of their specific hosts and hence colonize a narrow range of host species. Accordingly, an increase in host functional or phylogenetic dissimilarity is expected to increase the species diversity of parasitoids. However, the local diversity of parasitoids may be driven by the accessibility and detectability of hosts, both increasing with increasing host abundance. Yet, the relative importance of these two mechanisms remains unclear. We parallelly reared communities of saproxylic beetle as potential hosts and associated parasitoid Hymenoptera from experimentally felled trees. The dissimilarity of beetle communities was inferred from distances in seven functional traits and from their evolutionary ancestry. We tested the effect of host abundance, species richness, functional, and phylogenetic dissimilarities on the abundance, species richness, and Shannon-diversity of parasitoids. Our results showed an increase of abundance, species richness, and Shannon-diversity of parasitoids with increasing beetle abundance. Additionally, abundance of parasitoids increased with increasing species richness of beetles. However, functional and phylogenetic dissimilarity showed no effect on the diversity of parasitoids. Our results suggest that the local diversity of parasitoids, of ephemeral and hidden resources like saproxylic beetles, is highest when resources are abundant and thereby detectable and accessible. Hence, in some cases, resources do not need to be diverse to promote parasitoid diversity.

IV.2 Introduction

Most species worldwide are natural enemies of other species, as exemplified by parasitoids and parasites. Those species tend to be neither specialized on a single host species nor completely generalist, colonizing a set of similar and often closely related hosts (Strong *et al*., 1984). Natural enemies have hence adapted to overcome the chemical, morphological, physiological, and immunological defense characteristics of their host species, which can be phylogenetically conserved (Gross, 1993; Pennacchio & Strand, 2006; Strand & Pech, 1995). As a result, hosts with different functional characteristics or evolutionary ancestry tend to be exploited by different enemies (Frank, 1993). Hence, increasing phylogenetic or functional dissimilarity of host communities is thought to increase the species diversity of their enemies in a community (Schuler *et al*., 2015; Vialatte *et al*., 2010). This might be the case in systems in which functionally different hosts require fundamentally different adaptations from their enemies and the performance of an enemy to colonize one host species is traded off against its performance on colonizing another (Egas *et al*., 2005; Straub *et al*., 2011).

Enemy diversity may also depend on the detectability and accessibility of hosts: If hosts are hidden or sheltered, only the most specialized enemy species will be able to detect or use them (Price, 1973). Host detectability and accessibility, in turn, may increase with increasing host abundance. Host abundance increases host detectability by increasing olfactory, acoustical, or optical signals available for enemies (Yguel *et al*., 2014). Host abundance may also increase among-host competition forcing to leave the enemy-free space, that is, microsites or periods where or when hosts are inaccessible to enemies (Aukema & Raffa, 2000). Also, increased competition may require increased investment into competitiveness, binding energy that could otherwise be invested into defense against enemies (Bashey, 2015). In sum, low host abundance may reduce the diversity of natural enemies to a narrow subset of enemy species.

Parasitoids constitute several different taxonomic groups and are a key component of terrestrial ecosystems (Heraty, 2009). It is estimated that 10%–20% of all insect species belong to parasitoid Hymenoptera, representing the insect group with the highest species diversity worldwide (Forbes *et al*., 2018; Gaston, 1991). Comparable to parasites, the majority of parasitoid Hymenoptera is specialized on a certain set of hosts (Forbes *et al*., 2018) and exhibit a clear preference for one developmental stage over the others (Pennacchio & Strand, 2006; Strand & Pech, 1995; Wegensteiner *et al*., 2015), although many host species are so far unknown. As a result, a given parasitoid Hymenoptera species is typically most abundant only on one or a few focal host species.

Parasitoid Hymenoptera are one of the most important natural enemies of saproxylic beetle communities in forests, as mainly demonstrated for bark beetles (Curculionidae, Scolytinae) (Wegensteiner *et al*., 2015). Saproxylic beetles differ fundamentally in functional properties, such as in their preference for certain host tree species, diameters of deadwood, or their dependence on specific microclimatic conditions (Seibold *et al*., 2015a). Moreover, communities of saproxylic beetles change with succession during deadwood decomposition (Parisi *et al*., 2018). Many of these and other functional properties are phylogenetically conserved (Seibold *et al*., 2015b).The functional or phylogenetic dissimilarity of saproxylic beetle species might hence increase species diversity of parasitoid enemies. However, given that most saproxylic beetle species are extremely ephemeral and hidden, the diversity of their parasitoids might also increase with saproxylic beetle abundance.

We investigated communities of saproxylic beetle hosts and their associated parasitoid Hymenoptera. Both groups of insects were reared from experimentally felled trees during the early succession of deadwood. For each tree, the species diversity of saproxylic beetles and parasitoid Hymenoptera emerging from those beetles were quantified. In addition, the saproxylic beetle communities of each tree characterized according to their similarities across seven functional traits and their phylogenetic similarity, to measure functional and phylogenetic dissimilarities. Our aim was to test whether abundance or functional and phylogenetic dissimilarity of host communities determines the abundance and species richness of associated parasitoid Hymenoptera.

IV.3 Materials and methods

Study area and experimental design

Our study was conducted in the Bavarian Forest National Park, located in southeastern Germany. The park consists of approximately 24,850 ha of mountainous forests at elevations between 600 and 1,460 m a.s.l. Depending on the altitude, the annual average temperature ranges from 3.8 to 5.8°C. Yearly precipitation varies between 1,200 and 1,800 mm (Bässler *et al*., 2010a). Forest stands in higher elevations of the park area are naturally dominated by Norway spruce (*Picea abies*). Within the last two decades, extensive waves of natural disturbances have generated highly diverse deadwood structures, contributing substantially to partially more than 300 m3 of deadwood per hectare (Thorn *et al*., 2017).

Observational studies do naturally depend on the occurrence and spatial distribution of natural disturbances, which typically do not match the requirements of a standardized scientific study design (Lindenmayer *et al*., 2010). Also, often only a single host species is dominant, and results might be idiosyncratic to that species. Hence, we created artificial windthrows and applied bark treatments to create variance in the community composition of saproxylic beetles, that is, to avoid the dominance of the European spruce bark beetle (*Ips typographus*) (Figure IV.1c). *I. typographus* is the most important pest species of mature spruce stands throughout Eurasia with a preference for weakened or freshly dead Norway spruce trees (Wermelinger, 2004).

Our field experiment was established in April 2013. The design consisted of 12 artificial windthrows (plots), each composed of three pulled down mature Norway spruce trees with similar physical attributes (Figure IV.1a). Two trees per plot were uprooted and debranched, and their root plates were cut off. One tree was bark-scratched (disruption of the phloem every 3 cm), and a second tree was debarked (removal of all phloem). The remaining tree served as control. The minimum distance between plots was 200 m (for more details of the experimental design, see Thorn *et al.*, 2016a, 2016b. Within the conditions provided in our experiment, communities of beetles and parasitoids assembled naturally.

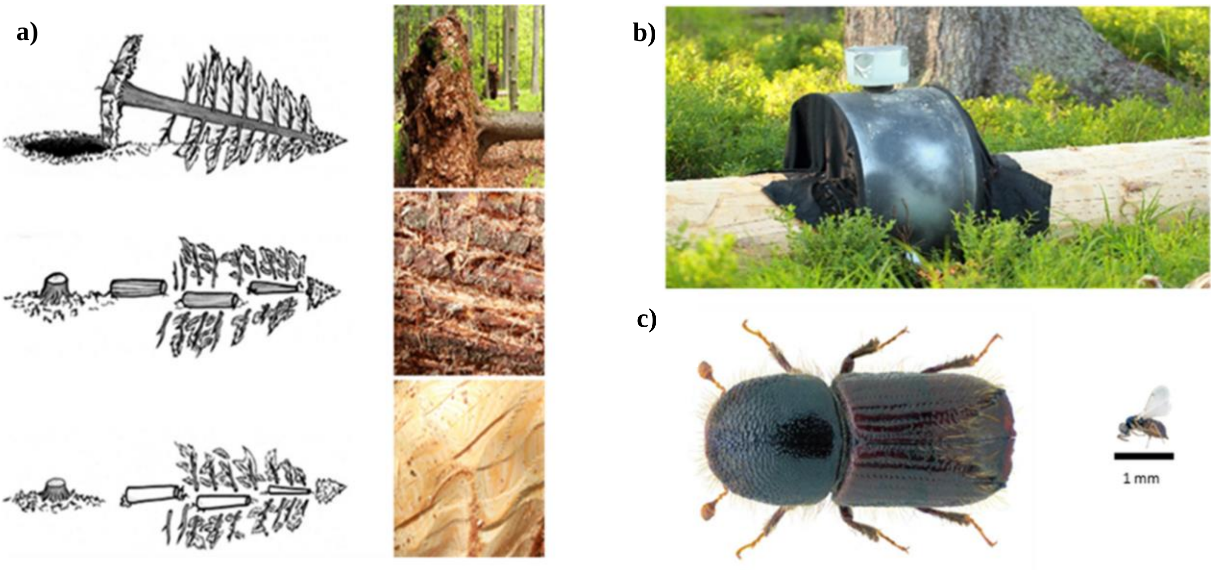

Figure IV.1: a) Different mechanical bark treatments used to alter abundance and species composition of saproxylic beetle communities. On each plot, one tree was fully debarked, one tree was bark-scratched (disruption of the phloem every 3 cm), and the third tree served as the control. **b)** Stem emergence trap used for sampling of saproxylic beetles and parasitoid Hymenoptera. **c)** The European spruce bark beetle (*Ips typographus*) and a parasitoid Hymenoptera (Superfamily Chalcidoidea) as representatives for the trapped species and analyzed communities (pictures were used after the Creative Commons license (CC BY-SA-2.0 and CC BY-3.0); copyright by U. Schmidt and M.A. Broussard)

Arthropod sampling

Communities of saproxylic beetles and parasitoid Hymenoptera were sampled by using one stem emergence trap per tree (Figure IV.1b), which were established from April to September 2014. Stem emergence traps are covering a given tree section and are only capturing individuals directly emerging from this section, representing the local community more complete the, for example, flight interception traps (Sverdrup-Thygeson & Birkemoe, 2009). To preserve species material for further steps, we used 90% ethanol and emptied traps monthly. All trapped beetles were identified to the species level according to Freude *et al.* (1963–1984) and classified as saproxylic according to Schmidl and Bussler (2004). To identify species of parasitoid Hymenoptera, one leg of each specimen was removed and submitted to the Canadian Centre for DNA Barcoding for DNA sequence analysis. DNA was extracted according to Ivanova *et al*. (2006), and standardized primer sets were used to amplify and sequence the 658-bp barcode region (Folmer *et al*., 1994; Hebert *et al*., 2003). The sequences were aligned with those in the Barcode of Life data system (Ratnasingham & Hebert, 2007). If the identification to the species level was not possible, barcoding data were used as molecular operational taxonomic units (MOTUs), which are represented by barcode index numbers and closely approximate species-level identifications (Ratnasingham & Hebert, 2013). Hereafter, MOTUs are included in "species" for simplicity. Single MOTUs were defined by a 97% sequence similarity. Species or MOTUs with sequences that matched those of parasitoids certainly not using coleopteran hosts according to Noyes (2019) and Yu *et al*. (2016) were excluded. The beetle data used in our paper are available online in Chao *et al*. (2019).

Host phylogeny and traits

We used the phylogenetic tree of European saproxylic beetles provided by Seibold *et al*. (2015b) according to the approach of Kuhn *et al*. (2011). The latter allows the input of partially resolved trees with known topology and node ages as constraints and applies a Markov chain Monte Carlo algorithm to permute polytomies using a constant-rate birth–death model. The phylogenetic tree was calibrated using 25 calibration points obtained from fossil records.

Functional dissimilarity was analysed using the resource-related and morphological traits of saproxylic beetles described by Gossner *et al.* (2013), Seibold *et al.* (2015b) , and Thorn *et al*. (2014). These databases represent the most comprehensive information about saproxylic beetle functional traits in Central Europe. Information on the mean diameter niche position (<15, 15–35, 35–70, >70 cm), the decay niche position (alive, freshly dead, initiated, advanced decomposition, extremely decomposed), and the canopy cover niche (open, semi-open, closed) was included, together with information on the preference of saproxylic beetle species for host trees (coniferous, broadleaved, both types of trees), the microhabitat guilds of larvae (wood and bark, cavities, fungi), the mean body size of single species, and the larval feeding type (detritivorous, mycetophagous, xylophagous, zoophagous). For the degree of phylogenetic correlation in functional traits, see Doerfler *et al*. (2020).

Dissimilarity of host communities

All statistical analyses were carried out in R version 4.0.3 (www.r-project.org). The phylogenetic tree of European saproxylic beetles was used to quantify phylogenetic dissimilarity based on the mean nearest taxon distance (MNTD), reflecting the mean distance separating each species from its closest relative in the same community. MNTD was additionally used to quantify the similarities among co-occurring species that may influence colonization by parasitoids. A value of MNTD less than zero thereby represents a clustered (i.e., similar) community of hosts, while a value greater than zero represents an overdispersed (i.e., dissimilar) community. To calculate MNTD, we first calculated the cophenetic distances between co-occurring species using the function `cophenetic´ from the R package `stats´. Because MNTD values can decrease as the number of species in a community increases, an abundance-weighted null model was applied to compare the observed MNTD values with those of 999 randomly generated communities containing the same number of species by using the function `ses.mntd´ from the R package `picante´ (Cavender-Bares *et al.*, 2006; Kembel *et al.*, 2010). This procedure resulted in a standardized effect size of MNTD that reflected the mean MNTD, that is, the phylogenetic dissimilarity of a beetle community standardized by species numbers. Standardized effect sizes of functional and phylogenetic diversities were only weakly correlated (Pearson's r: 0.29).

The functional dissimilarity of saproxylic beetle communities was calculated using the same procedure as described above, except that the distance matrices of traits were calculated as Euclidean (numeric variables) and Gower (non-numeric or in combination with numeric variables) distances using the function `daisy´ from the R package `cluster´ (Gower, 1971).

Statistical analyses

The effects of abundance, species richness, phylogenetic dissimilarity, and functional dissimilarity of saproxylic beetle communities were tested on the abundance, species richness, and Shannon-diversity of parasitoids as response variables. We standardized the number of sampled saproxylic beetle species to 0.95 sample completeness using a rarefaction/extrapolation framework according to Hsieh *et al.* (2016), implemented in the R package `iNext´, We estimated the sample coverage of saproxylic beetles and parasitoid Hymenoptera by the same approach.

The effect of saproxylic beetle communities on the abundance of parasitoids was tested by applying a generalized linear mixed model with poisson error distribution by using the R package `lme4´ (Bates *et al.*, 2015). This model included the abundance of parasitoids as response variable and the log-transformed abundance, species richness, functional dissimilarity, and phylogenetic dissimilarity of the respective host beetle communities as predictor variables. Furthermore, we included the plot as random effect to account for the nested study design (Bolker *et al*., 2009) and the sample id to account for possible Poisson overdispersion (Elston *et al*., 2001). We used the same model formula to model species numbers and additionally included the log-transformed abundance of parasitoid Hymenoptera to the model. Shannon-diversity of parasitoids was modelled using the same model formula as for species numbers but a Gaussian error distribution.

IV.4 Results

Our dataset included 15,516 individuals of saproxylic beetles from 106 species and 146 individuals from 44 species of parasitoids (Table IV.1), corresponding to a 0.93% rate of successful parasitization. The mean species number per log was 23.61 ± 7.5 species for saproxylic beetles and 2.64 ± 2.6 for parasitoids. Species accumulation curves revealed a high sample coverage of both, saproxylic beetles and parasitoid Hymenoptera (Figure IV.2).

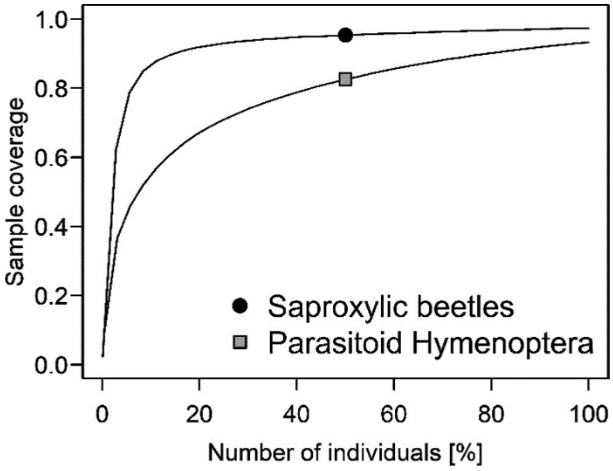

Figure IV.2: Sample coverage of saproxylic beetles and parasitoid Hymenoptera based on rarefaction/extrapolation up to twice the actual sampling effort. Note that the number of sampled individuals has been transformed to percentage for better comparability.

Saproxylic beetles were dominated by bark beetles (Curculionidae, Scolytinae), encompassing 10,869 individuals from 18 species. The most abundant beetle species, *Trypodendron lineatum*, was represented by 7,496 trapped individuals. *Ips typographus* was trapped by 824 (control trees), 180 (bark-scratched trees), and 19 (debarked trees) individuals, respectively. Parasitoids were recorded from 11 families, dominated by Pteromalidae (40 individuals, 10 species), Platygastridae (36 individuals, 10 species), and Braconidae (33 individuals, 6 species). Many of the parasitoids recorded in our study were rare: 36 species of parasitoids with ≤3 individuals contributed 66 of the 146 sampled individuals (Table IV.1).

Table IV.1: Species of parasitoid Hymenoptera recorded in our study with their respective abundances.

ID	Scientific name	Abundance
Braconidae (6 species/33 individuals)		
BOLD:AAU9839	*Chelonus* sp.	1
BOLD:ACM7216	*Ropalophorus clavicornis*	1
BOLD:ACM7563	*Dendrosoter middendorffii*	5
BOLD:ACQ8673	Brachistinae	1
BOLD:ACQ9535	*Cosmophorus regius*	2
BOLD:ACQ9771	*Blacus* sp.	23
Ceraphronidae (3 species/5 individuals)		
BOLD:ACF6025	*Aphanogmus* sp.	3
BOLD:ACG4508	*Aphanogmus* sp.	1
Ceraph_01	*Aphanogmus* sp.	1
Diapriidae (2 species/2 individuals)		
BOLD:ACG4055	*Pantoclis* sp.	1
Diapri_01	*Trichopria* sp.	1
Eulophidae (4 species/7 individuals)		
BOLD:ACQ8898	*Necremnus croton*	2
BOLD:ACQ9006	*Necremnus leucarthros*	3
Euloph_01		1
Euloph_02		1
Eupelmidae (1 species/2 individuals)		
Eupelm_01		2
Eurytomidae (1 species/3 individuals)		
BOLD:ACM7745	*Eurotoma arctica/afra*	3
Figitidae (1 species/1 individual)		
BOLD:ACQ9714	Eucoilinae	1
Ichneumonidae (4 species/13 individuals)		
BOLD:ABU6543	*Enclisis vindex*	2
BOLD:ACQ9146	*Phrudus monilicornis*	3

BOLD:ACR0681	*Phradis* sp.	1
BOLD:ACR0964	*Rhimphoctona teredo*	7
Platygastridae (10 species/36 individuals)		
BOLD:AAN8098	*Telenomus* sp.	9
BOLD:ACC2809	Scelioninae	2
BOLD:ACF7380		1
BOLD:ACF9487		2
BOLD:ACI4334	*Telenomus* sp.	10
BOLD:ACI4527	*Telenomus* sp.	1
BOLD:ACI9091	*Telenomus* sp.	4
BOLD:ACI9128	*Telenomus* sp.	3
BOLD:ACR1479		2
BOLD:ACR1888		2
Proctotrupidae (2 species/4 individuals)		
BOLD:ACR1488		2
BOLD:ACR1985		2
Pteromalidae (10 species/40 individuals)		
BOLD:AAN8215	*Pteromalus* sp.	2
BOLD:AAZ7417	*Mesopolobus gemellus*	3
BOLD:ACA9177		1
BOLD:ACM7334	*Roptrocerus mirus*	15
BOLD:ACM7652		2
BOLD:ACQ8466	*Dinotiscus eupterus*	3
BOLD:ACQ8826	*Holcaeus compressus*	7
BOLD:ACQ9876	*Perniphora robusta*	3
Pterom_01		3
Pterom_03		1

Abundance of parasitoids increased with increasing abundance and species richness of saproxylic beetles (Figure IV.3a). Species numbers and Shannon-diversity of parasitoid Hymenoptera strongly increased with increasing abundance of parasitoid Hymenoptera (Figure IV.3b, c). Shannon-diversity of parasitoid Hymenoptera increased with increasing host abundance (Figure IV.3c). We did not find any significant effect of functional or phylogenetic dissimilarity on any of our response variables (Figure IV.3).

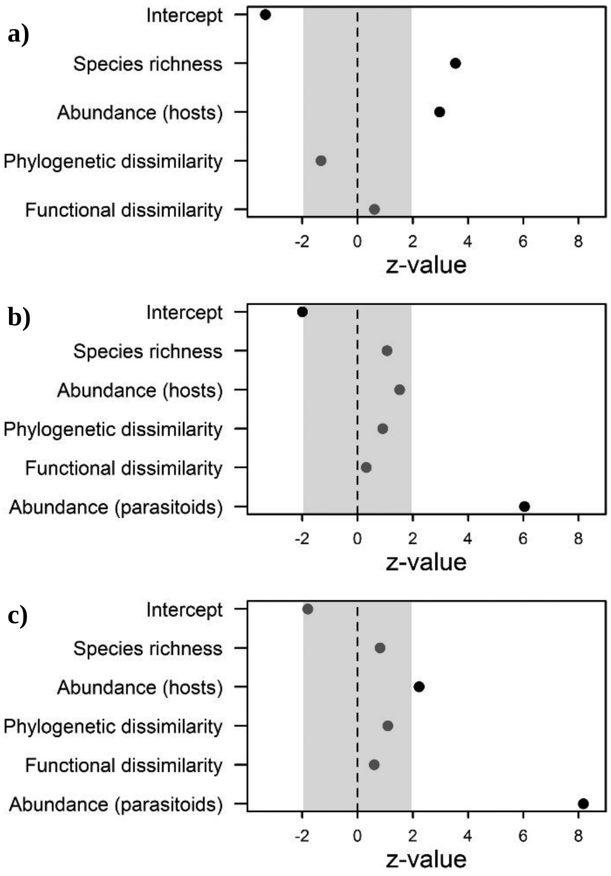

Figure IV.3: Relative effect strengths (z-values) of predictors on **a)** abundance of parasitoid Hymenoptera, **b)** species numbers of parasitoid Hymenoptera, and **c)** Shannon-diversity of parasitoid Hymenoptera. Gray shading indicates the range of non-significant z-values, significant effects depicted by black dots.

IV.5 Discussion

Our results indicate that abundance and species richness in communities of parasitoid Hymenoptera increase with increasing abundance of hosts, whereas functional and phylogenetic dissimilarities of host communities were of minor importance. Furthermore, species numbers of parasitoids were strongly promoted by their abundance, which in turn increases with species richness of hosts. Thereby, our results do not support that functional or phylogenetic dissimilarity of hosts begets the diversity of parasitoids within deadwood objects, but rather point toward an abundance-driven system.

The increasing abundance and species richness of parasitoids with increasing abundance of their saproxylic beetle hosts are in line with the »more individuals hypothesis«, an extension of the »species-energy theory« (Clarke & Gaston, 2006; Schuler *et al.*, 2015). The »more individuals hypothesis« predicts an increase in the abundance and consequently in species richness of a given species group (i.e., parasitoids) in response to an increase in the availability of resources (i.e., hosts). The »more individual's hypothesis« is valid as long as species use different niches and do not rely on the same resources (MacArthur & MacArthur, 1961; Tews *et al*., 2004). In our study system, an increasing abundance could increase the detectability (Vinson, 1998) and accessibility (Price, 1973) of saproxylic beetle hosts.

In our study system, host accessibility may be limited, given the short spatiotemporal window during which a specific developmental stage of a host exists. Furthermore, parasitoids may be limited to a specific set of host species and do not utilize patches with extremely low host abundance (Hassell, 2000; Murdoch, 1977).

High host abundances may force some hosts into enemy-exposed microenvironments. In our study system, this could apply to bark beetles, which reached highest abundances of potential hosts and then might be forced to occupy parts of the tree trunk, which are easier to access to parasitoids (Aukema & Raffa, 2000).

Higher abundances of hosts might also increase the detectability that is the olfactory signal to parasitoids, since saproxylic beetles, especially bark beetles, emit sex pheromones (Vega & Hofstetter, 2015). Furthermore, at extremely high abundances, bark beetles can emit anti-aggregation pheromones (Sun *et al*., 2006). Such pheromones might additionally increase host detectability at high abundances. Overall, abundance of bark beetles might render them distinctly more detectable or accessible to a larger number of parasitoid species and thereby increase their species diversity.

We did not find any effect of functional or phylogenetic dissimilarity of hosts on parasitoid communities (Figure IV.3). Functional dissimilarity might reflect to some degree functional identity. If there is one dominant functional group, such as in our case bark beetles, then a greater functional similarity may reflect the dominance of that group. Specifically, our samples were composed of species colonizing mainly the phloem of recently killed Norway spruce. Specialization on particular host groups may reflect constraints on, for example, ovipositor length. For example, bark thickness limits parasitization by *Caenopachys hartigii* (Braconidae, Doryctinae) (Mancini *et al*., 2003). Thus, host species that do not feed directly under the bark or other superficial parts of deadwood might not be reachable by this enemy. A highly abundant bark beetle species in our study was *T. lineatum*, which create galleries into sapwood, where it might be difficult to access for parasitoids. Indeed, only few species of parasitoids enter bark beetle galleries for oviposition (Vega & Hofstetter, 2015).

It is possible that the effect of functional identity overlays and partly conceals the effect of functional dissimilarity, explaining why we did not find any effect of functional dissimilarity. Despite we used the most comprehensive database of saproxylic beetles, we are still lacking information about, for example, temporal occurrence of saproxylic beetles. An extension of our trait database by such information may hence change the relative importance of functional dissimilarity. Phylogenetic dissimilarity did not show a significant effect on parasitoid abundance (Figure IV.3). One of the reasons for the lacking effect of phylogenetic dissimilarity might be that closely related beetle hosts occur in high abundances, such as bark beetles in our study system. This is ultimately caused by the fact that host beetle communities cannot be established in a fully experimental design that is, covering a range of phylogenetic dissimilarity, due to their host tree specializations. Moreover, for a set of locally coexisting species, phylogenetic dissimilarity may not necessarily reflect the dissimilarity of functional traits (Prinzing *et al.*, 2008).

Overall, our study suggests that resource diversity does not mandatory begets the diversity of local enemy communities. This intuitive hypothesis implicitly assumes that any given type of resources is detectable and accessible to the consumers. In that case, a diverse set of resources can be used by a diverse set of consumers. However, if resources are hosts that are ephemeral and hidden, they may easily remain undetected by or inaccessible to many potential parasitoids. Only at high host abundance, detection, and access may become possible for many parasitoid species, leading to an increase of parasitoid diversity with host abundance.

IV.6 Acknowledgements

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IV.7 Supporting Information

All Supporting Information are electronically attached and public available online.

Chapter V: General discussion

Considering the current situation of global forest ecosystems as well as future challenges by increasing human demands and climate change, effective and applicable conservation strategies are growing in importance to counter the loss of biodiversity (Hooper *et al*., 2005; Nocentini *et al*., 2017). Deadwood can be here considered as a key element, as it is hosting a significant proportion of species and contributes to essential ecosystem processes (Seibold *et al*., 2021; Speight, 1989; Stokland *et al*., 2012). Hence, a detailed understanding of saproxylic species and their interactions can help to derive evidence-based conservation measures and to improve existing conservation strategies in a multifunctional forest landscape matrix (van der Plas *et al*., 2017).

In chapter II, I confirmed that sun exposure and tree species are both important determinants for the diversity of saproxylic species. However, their impact strongly differed between saproxylic beetles, wood-inhabiting fungi, and spiders as well as deadwood diameters. Based on the six included tree species and the applied random-drawing procedure, I also identified that combinations of broadleaved and coniferous as well as hard- and softwood tree species are needed to support high levels of saproxylic species diversity.

To determine the conservational importance of single tree species more in detail, I experimentally sampled further 42 different tree species for saproxylic beetles, considering dominant as well as subdominant, silviculturally unimportant, rare, native, and non-native tree species (chapter III). The results showed a strong variation of species diversity among single tree species, while a few tree species hosted the majority of saproxylic beetle species, especially *Quercus* sp.. However, tree species with a medium or low overall diversity were of high importance for red-listed beetle species as well. This demonstrates that such tree species, mostly subdominant, silviculturally less important or rare, should not be neglected within conservation strategies.

Lastly, I was interested in the diversity of parasitoid Hymenoptera as one of the cryptic saproxylic taxa in interaction with the diversity of saproxylic beetles as their hosts (chapter IV). Surprisingly, communities of parasitoid Hymenoptera were not affected by the functional and phylogenetic dissimilarity of host communities but by host abundance. The abundance of parasitoid Hymenoptera additionally increased with increasing host species richness. Therewith, the results indicate an abundance-driven system in which the general availability, not necessarily the diversity of potential hosts, is decisive.

V.1 Impact of sun exposure and tree species

With this thesis I confirmed the high importance of sun exposure and tree species for the diversity of saproxylic species. In chapter II, I first revealed that all analysed saproxylic taxa were affected by sun exposure, but they were affected in different directions. The alpha-diversity of saproxylic beetles and spiders in logs was higher under sun-exposed compared to canopy-shaded and artificially shaded conditions, while wood-inhabiting fungi reached a higher alpha-diversity under artificially shaded than under sun-exposed and lastly canopy-shaded conditions. Higher diversities of saproxylic arthropods under sun-exposed conditions are also reported by a variety of other studies (Lindhe *et al*., 2005; Seibold *et al*., 2016b; Thorn *et al*., 2016a). Their preference for sun-exposed deadwood is mainly attributed to significant differences in daily temperature between sun-exposed and shaded deadwood. Higher temperatures under sun-exposed conditions might be able to benefit metabolic reactions of poikilothermic saproxylic species and thus their activity (Brown *et al*., 2004). Furthermore, measurements of surface temperatures on logs revealed a higher diversity of temperature zones on sun-exposed logs compared to shaded deadwood, offering a higher number of different niches (Müller *et al*., 2020). In contrast to saproxylic arthropods, wood-inhabiting fungi benefit from a combination of higher temperatures and humidity is, as both factors are determining fungal growth and activity (Venugopal *et al*., 2016).

The comparison between saproxylic beetles in logs and branches furthermore revealed differences between deadwood diameters. The reduced alpha-diversity of saproxylic beetles in sun-exposed branches is presumably the effect of their lower buffer effect against extreme microclimatic conditions compared to logs (Bässler *et al*., 2010b; Siitonen & Ranius, 2015). Those conditions are challenging the colonization and successful development of saproxylic species. However, a missing effect of sun exposure on species diversity was detected in the study of chapter III. Branches used here had a larger diameter than those in chapter II and were therewith intermediate between the both object types used in chapter II. Thus, my findings for sun exposure indicate that the impact of this determinant is taxa- and also diameter-dependent.

In contrast to sun exposure, which revealed an impact on all investigated saproxylic taxa in the study of chapter II, there were differences for the impact of tree species, which only affected saproxylic beetles and wood-inhabiting fungi. Both groups are obligate saproxylic and cannot exists without deadwood resources. In contrast, spiders are using deadwood only facultatively as foraging ground (Seibold *et al*., 2016a). Furthermore, the difference of spiders might be the result regarding their higher trophic grading in the saproxylic food web. For instance, Wende *et al*. (2017) demonstrated a higher host tree specificity of xylophagous saproxylic beetles and a lower host tree specialization of zoophagous beetles.

Even if my thesis analysed the impact of sun exposure and tree species on taxonomic diversity only, both determinants are also able to affect the functional and phylogenetic diversity of saproxylic communities (Günter, 2019; Heikkala *et al*., 2016; Thorn *et al*., 2018a). However, different measurements of diversity are not affected in the same direction, for instance shown by Günther (2019). Günther (2019) analysed the same data of saproxylic beetles in logs used in chapter II. As opposed to taxonomic diversity, the functional diversity of saproxylic beetle communities was here lower under sun-exposed conditions, while there is no effect on the phylogenetic diversity. This finding indicates that saproxylic beetles found under sun-exposed conditions are functionally more similar than expected by chance, which might indicate an ecological filtering towards sun-adapted species of saproxylic beetles (Heikkala *et al*., 2016). These sun-adapted species are recruited from all lineages in the phylogenetic tree, explaining the missing effect on phylogenetic diversity of saproxylic beetle communities. According to the results of chapter IV and the revealed missing effects of functional and phylogenetic dissimilarity, the impact of sun exposure and tree species on the functional and phylogenetic diversity of saproxylic beetles do not seem to be indirectly transferred to higher trophic levels via inter-trophic interactions. However, the need for further analyses of direct and indirect effects of determinants of saproxylic biodiversity on different trophic levels still remains (see V.4).

V.2 Importance of tree species diversity and non-native tree species

Chapters II and III of the present thesis demonstrated especially for saproxylic beetles differences in species diversity and community composition among compared tree species. Furthermore, I revealed in chapters II and III that it is not enough to promote deadwood from single tree species only, but that rather the full range of local native woody plant diversity needs to be considered. However, this is currently not taken into account by most practised conservation strategies, as they mainly actively promote deadwood from dominant broadleaved tree species, mostly beech (*Fagus sylvatica*). Basically, this approach is not absolutely wrong, as communities of saproxylic beetles are assumed to show a preference for local dominant tree species, which are generating the highest amount and diversity of deadwood structures (Brändle & Brandl, 2001; Bussler *et al*., 2011). However, some dominant tree species like oak (*Quercus sp*.) or Norway spruce (*Picea abies*) are generally excluded from deadwood enrichment by policy and reasons of forest protection (Alexander, 2016; Brown *et al*., 2015; Gößwein *et al*., 2017; Thorn *et al*., 2016b). Especially in the case of *Quercus sp*. this does not seem to be necessarily justified. *Quercus sp*. is hosting the highest number of saproxylic beetle species compared to other tree species in Central Europe (see e.g. III.4) and has an evidenced relevance for conservation (Brändle & Brandl, 2001; Jonsell *et al*., 1998; Müller & Gossner, 2007; Walentowski *et al*., 2014). Deadwood from *P. abies*, where the protection against the European spruce bark beetle (*Ips typographus*) is the main problem, could be further promoted by using alternative techniques like bark-scratching (Hagge *et al*., 2019b; Thorn *et al*., 2016b).

With the community analyses in chapters II and III, I showed that coniferous tree species are of equal importance for the diversity of saproxylic species compared to broadleaved tree species. The analyses revealed distinct differences in the composition of hosted communities of saproxylic beetles and wood-inhabiting fungi between both groups of tree species (see Supporting Information S6 of chapter II, Figure III.3). The enrichment of deadwood from only broadleaved tree species is therewith not sufficient, as saproxylic species specialised on coniferous tree species are disadvantaged. As revealed by the random-drawing procedure in chapter II, the most effective combinations of tree species should include broadleaved as well as coniferous tree species, as together they host the most complementary saproxylic communities (see Figure II.4).

Differences between saproxylic communities of single tree species, including the differences between broadleaved and coniferous tree species, are as known caused by different tree-specific properties (Moll *et al*., 2018; Purahong *et al*., 2018c; Yang *et al*., 2021). For instance, in the study of chapter II, the faster decay rates of hornbeam (*Carpinus betulus*) and aspen (*Populus tremula*) compared to *F. sylvatica* and sessile oak (*Quercus petraea*) are a probable explanation for the relatively high diversity of saproxylic species in logs of both tree species (Gossner *et al*., 2016; Kahl *et al*., 2017; Müller *et al*., 2015b). In a comparable period of time, such a faster decay rate enables the faster formation of different niches and thus habitats for different saproxylic species, but it also shortens the longevity of a deadwood object as a suitable resource. As inferred in chapter II, the separation into hard- and softwood tree species is therefore a possible attempt to consider the diversity of tree-specific properties within conservation strategies for saproxylic species. However, considering that tree-specific properties are much more multifaceted, comprising various anatomical, physicochemical and other characteristics, such a separation needs to be extended and no tree species should generally be excluded from deadwood enrichment.

Beside dominant tree species, subdominant, silviculturally unimportant and rare tree species are also able to contribute to the variety of wood-related tree-specific properties, partially with unique combinations of properties. As shown in chapter III, such tree species are also able to host high diversities of saproxylic beetles (e.g. apple (*Malus domestica*) or small-leaved lime (*Tilia cordata*)) or are, even if they host a comparable medium or low overall diversity, equally important for red-listed species (e.g. *A. glutinosa*, *S. caprea*, or *S. aucuparia*), which are frequently host tree specialists. Detected examples in chapter III were for instance *Rusticoclytus pantherinus* (Cerambycidae, Red List Category “0”) and *Agrilus guerini* (Buprestidae, Red List Category “2”) (StMUGV, 2005), feeding exclusively on goat willow (*Salix caprea*).

The last facet of tree species diversity analysed within this thesis was the importance of non-native tree species for saproxylic beetles. As explained in the beginning, a variety of such tree species has already been introduced to forestry (Schmid *et al*., 2014; Vítková *et al*., 2017) and the ongoing climate change has once again revived discussions about a reinforced introduction (Bolte *et al*., 2009; Brus *et al*., 2019; Krumm & Vitkova, 2016; Mette *et al*., 2021). From the point of view of nature conservation this has to be seen with caution. For saproxylic species, the impact of non-native tree species is mostly poorly known and existing studies provide a mixed evidence (Bouget *et al*., 2020; Lanta *et al*., 2021; Ulyshen *et al*., 2018). Also with the results of chapter III, it is not possible to take a clear position on whether non-native tree species are acceptable or detrimental to conservational interests. In my study, I showed that in general non-native tree species are able to host high diversities of saproxylic beetles (see Figure III.2), but the community composition differs compared to native tree species (see Supporting Information S7 of chapter III). The most important point I detected was that non-native tree species do not seem to necessarily have the same importance for red-listed saproxylic beetles. Three tree species originating from Northern America (Weymouth pine (*Pinus strobus*), Douglas fir (*Pseudotsuga menziesii*), and black locust (*Robinia pseudoacacia*)) hosted no red-listed species, whereas all tree species originating from Southern Europe hosted red-listed saproxylic beetles and Turkey oak (*Quercus cerris*) the most in the whole study (see Figure III.2). Thus, non-native tree species with a natural distribution in Europe might have an advantage. They might be also more accessible for saproxylic beetles species with a stronger host tree specificity due to their lower phylogenetic proximity to native tree species and the resulting similarity of wood-related properties (Branco *et al*., 2015).

V.3 Improvement of conservation strategies

Probably the most challenging task of modern forest management is to support the multifunctional role of forests and thereby simultaneously to satisfy economic and ecological demands (Freer-Smith & Carnus, 2008; Nocentini *et al*., 2017; Niemelä *et al*. 2005; van der Plas *et al*., 2017). Thus, a main objective of this thesis was to improve existing conservation strategies for saproxylic species by deriving applicable measures that require a minimum of additional effort. Especially chapters II and III provided different recommendations for the inclusion of deadwood heterogeneity by controlling sun exposure and tree species diversity as two of the main determinants of saproxylic species. The recommended measures are applicable in both, active and passive approaches of integrative conservation strategies. All measures are addressed to conservation practitioners, local foresters, governmental authorities and other decision makers and aim to provide guidance for future actions in temperate forests.

Overall, the given recommendations are highlighting the general importance of integrating sun exposure and tree species diversity into effective conservation strategies alongside the sole need for quantitative deadwood enrichment. The results of this thesis are enhancing recent conservation strategies by providing more detailed recommendations about combinations of sun exposure and tree species as well as the importance of single tree species for conservation:

(1) Sun exposure as an important determinant of saproxylic species diversity and community composition should be promoted along the full range of canopy openness. Due to the lack of sun-exposed conditions in modern production forests, deadwood of particular large diameters is needed to be enriched at sun-exposed forest edges or with help of coppicing, gap cutting, and leaving of natural disturbances (Figure V.1).

(2) Tree species diversity must be increasingly incorporated into deadwood enrichment as communities of saproxylic beetles and wood-inhabiting fungi vary distinctly between tree species. As evaluated in chapter II, the most effective combinations of tree species should consist of broadleaved and coniferous as well as hard- and softwood tree species, as they together host the most complementary saproxylic communities.

(3) To protect the diversity of saproxylic beetles, especially red-listed species and host tree specialists, the full range of local native woody plant diversity should be considered, with a specific focus on subdominant, silviculturally unimportant, and rare tree species. Pioneer species and tree species of low economic value should be allowed to undergo

natural senescence and decay. Furthermore, tree species that prefer sun-exposed conditions can be promoted by the creation of sun-exposed forest structures as recommended above. The enrichment of deadwood from non-native tree species should not be given priority, as their impact on saproxylic species is not finally clarified.

(4) In addition to the importance of sun exposure and tree species, which was a main focus of this thesis, chapters II and III also revealed that the spatial distribution of deadwood is a significant driver of beta-diversity. Hence, deadwood should be enriched on a landscape-level to cover different local conditions, e.g. respective microclimate. Furthermore, an enrichment on landscape-level guarantees an area-wide availability of deadwood and thus the connectivity of deadwood resources as well as local populations of saproxylic species.

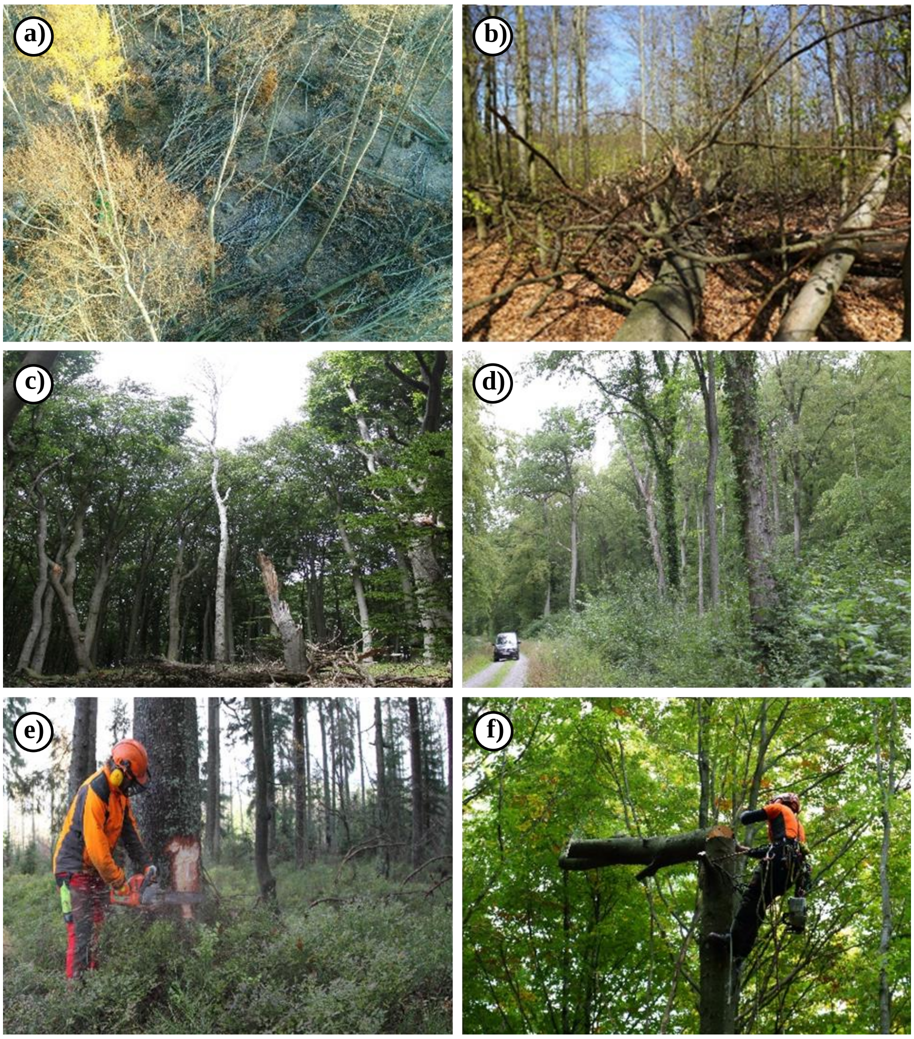

Figure V.1: Different methods of passive and active deadwood enrichment, which can increase the amount of deadwood as well as deadwood heterogeneity. All methods can be regularly incorporated into forest regimes: **a)** leaving of small scale windthrows, **b)** leaving of tree parts after harvest operations, **c)** gap cutting of small tree groups, **d)** opening of forest edges, **e)** tree girdling, and **f)** pollarding. The figure is redrawn and expanded after Thorn *et al.* (2020).

V.4 Future research

Although a variety of different abiotic and biotic determinants has been identified to affect diversity patterns of saproxylic species, a mechanistic and detailed understanding is still incomplete (reviewed in Seibold *et al*., 2015a). These gaps allow different starting points to enhance the ecological knowledge as well as to advance recommendations for conservation. Based on the findings of this thesis and latest research questions, the following main points may be addressed in future scientific studies:

(1) Studies analysing the impact of tree species on saproxylic biodiversity commonly use the host tree identity mainly as the only proxy to explain differences (e.g. in chapters II and III). However, the host tree identity is only summarizing a manifold of anatomical, physicochemical, and other tree-specific properties, whose variability is in turn responsible for the host tree specificity of individual saproxylic species, ultimately determining species richness and community composition. Beside different metabolites acting as defence mechanisms, only single other wood-related properties and their importance have been identified so far. This is mainly due to the lack of comparable measurements across different tree species and the small set of analysed wood-related properties. Most existing studies, mainly investigating molecular community data of bacteria and wood-inhabiting fungi, have revealed a distinctive impact of pH-value, wood density, lignin, and water content on community composition (Moll *et al*., 2018; Purahong *et al*., 2018c; Rajala *et al*., 2012). The recent study of Yang *et al*. (2021) is here an exception, as wood-inhabiting fungi were analysed by mapping of basidiomes and by measuring 20 different wood-related properties (anatomical and physicochemical). This study revealed, that fungal communities are also strongly driven by the nutritional value of wood as well as chemical and physical defence factors, which are related to the phylogenetic correlation (Gymnosperms versus Angiosperms). However, comprehensive data and studies of wood-related properties are further rare and analyses for most saproxylic taxa, e.g. saproxylic beetles or higher trophic levels missing, linking to the next point of research interest.

(2) Investigations on determinants of saproxylic species are more or less limited to certain, well known saproxylic taxa, preventing the detection of various direct and indirect effects of these determinants as well as the differences between taxa and trophic levels of the saproxylic food web (see II.4; Müller *et al*., 2020). However, individual studies as in chapters II and III suggest that determinants such as the host tree identity affect

saproxylic species directly depending or feeding on wood much more than e.g. mycetophagous or zoophagous species (Wende *et al.*, 2017). Moreover, the quantification of interactions among different trophic levels is an important part of modern ecology, but only a few previous studies have analysed such interactions within the saproxylic food web, e.g. between wood-inhabiting fungi (Fukami *et al.*, 2010) or wood-inhabiting fungi and saproxylic invertebrates (Seibold *et al.*, 2019b; Six, 2012; Skelton *et al.*, 2020). These studies have revealed a variety of multifaceted interactions determined by priority and top-down effects (Crowther *et al.*, 2013; Fukami *et al.*, 2010). In order to work on both topics together, a comprehensive experimental approach comparable to chapters II and III is needed, which allows to disentangle the relative impact of different determinants on multitaxa and multitrophic diversity. Furthermore, advanced methods, such as meta-barcoding for cryptic taxa, need to be included.

(3) In a macroecological perspective, patterns in biodiversity are commonly linked to energy resources, which in turn are following geographical gradients (Gaston, 2000; Willig *et al.*, 2003). The availability of energy is determined by different abiotic variables as the amount of precipitation or the mean annual temperature (Brown *et al.*, 2004; Clarke & Gaston, 2006). Within saproxylic species, for instance, such patterns were observed for the distribution of functional diversity in communities of saproxylic beetles and wood-inhabiting fungi (Hagge *et al.*, 2019a). Furthermore, basidiomes of wood-inhabiting fungi revealed a higher darkness with increasing latitude (Krah *et al.*, 2019), a pattern that was also found for many other poikilothermic taxa, e.g. in moths (Heidrich *et al.*, 2018). A higher body darkness enables a better absorption of solar energy to compensate colder climate conditions by increasing body temperature, while it is obstructive in warmer regions by restricting metabolic reactions at a certain point (Brown *et al.*, 2004). Thus, in addition to the macroclimate, the energy availability for saproxylic species is significantly influenced by the local microclimate and hence sun exposure (Brown *et al.*, 2004). For saproxylic species, a higher sun exposure often results in a higher species diversity (see II.4; Lindhe *et al.*, 2005; Seibold *et al.*, 2016a; Thorn *et al.*, 2016a), but so far it is unknown if this can be generalised for all climatic regions. Potentially, sun-exposed deadwood structures might be of less importance in southern regions but different determinants of deadwood heterogeneity could be of higher relevance in Northern Europe (Chiari *et al.*, 2012). This would make prospective adaptations of recommendations and conservation strategies according to climate conditions necessary.

Here, an intercontinental approach across Europe is needed to provide further information.

V.5 Conclusions

Based on the findings of chapters II, III, and IV, the most important conclusions of the present thesis are:

(1) Sun exposure and tree species are important determinants of saproxylic species, but their impact is strongly context-dependent and differs among respective saproxylic taxa and deadwood diameters.

(2) Species diversity and community composition of saproxylic beetles and wood-inhabiting fungi differ between tree species and mainly broadleaved and coniferous tree species. Combinations of tree species hosting the highest diversity of saproxylic species are composed of broadleaved and coniferous as well as hard- and softwood tree species.

(3) Large parts of saproxylic beetle diversity during early decay are hosted by a few tree species, but tree species with a comparatively low overall diversity are likewise important for red-listed saproxylic beetle species as well. Tree species that are important for the conservation of saproxylic beetles are not only represented by dominant, but also subdominant, silviculturally unimportant, and rare tree species.

(4) Communities of parasitoid Hymenoptera are not affected by the phylogenetic and functional diversity of hosts but by host abundance and thus general host availability.

(5) Effective conservation strategies for saproxylic species need to consider a quantitative deadwood enrichment on a landscape-level but they furthermore have to support the full range of sun exposure conditions, mainly by the creation of sun-exposed structures, as well as by involving the full range of local native woody plant diversity.

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Appendix

A.1 Affidavit

Affidavit

I hereby declare that my thesis entitled: **„Determinants of saproxylic biodiversity and conclusions for conservation“** is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Besides I declare that if I do not hold the copyright for figures and paragraphs, I obtained it from the rights holder and that paragraphs and figures have been marked according to law or for figures taken from the internet the hyperlink has been added accordingly.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation: **„Einflussfaktoren auf xylobionte Artenvielfalt und Rückschlüsse für den Naturschutz“**, eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Weiterhin erkläre ich, dass bei allen Abbildungen und Texten bei denen die Verwertungsrechte (Copyright) nicht bei mir liegen, diese von den Rechtsinhabern eingeholt wurden und die Textstellen bzw. Abbildungen entsprechend den rechtlichen Vorgaben gekennzeichnet sind sowie bei Abbildungen, die dem Internet entnommen wurden, der entsprechende Hypertextlink angegeben wurde.

Würzburg, 15.03.2022

Signature/Unterschrift

A.2 Author contributions

Chapter II

Vogel, S., Gossner, M.M., Mergner, U., Müller, J, & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. *Journal of Applied Ecology, 57*(10), 2075–2085. doi: 10.1111/1365-2664.13648.

Corresponding author: S. Vogel Impact factor: 5.84 (2019)

MG and JM designed the experiment. SV, UM, JM, and ST established the study. SV collected the data. SV, JM, and ST analysed and interpreted the data. SV led the writing of the manuscript and wrote the first draft. All co-authors contributed to improve later drafts.

Chapter III

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2020). Diversity and conservation of saproxylic beetles of 42 European tree species – an experimental approach from early successional stages of branches. *Insect Conservation and Diversity*, *14*(1), 132-143. doi: 10.1111/icad.12442.

Corresponding author: S. Vogel Impact factor: 2.73 (2019)

SV, SF, and JM developed the idea and designed the experiment. SV, SF, and ES established the study. SV collected the data. HB determined the species. SV and ST analysed and interpreted the data. SV led the writing of the manuscript. All co-authors contributed to improve later drafts.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2021). Corrigendum: Diversity and conservation of saproxylic beetles of 42 European tree species – an experimental approach from early successional stages using branches. *Insect Conservation and Diversity, 14*(3), 412-414. doi: 10.1111/icad.12496.

Corresponding author: S. Thorn Impact factor: 2.73 (2019)

SV verified the data. ST reanalysed the data. ST led the writing of the manuscript. SV and JM contributed to improve the final draft.

Chapter IV

Vogel, S., Prinzing, A., Bussler, H., Müller, J., Schmidt, S. & Thorn, S. (2021) Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood. *Ecology and Evolution*, *11*(11), 6881-6888. doi: 10.1002/ece3.7535.

Corresponding author: S. Thorn Impact factor: 2.39 (2019)

JM and ST designed the experiment. JM and ST established the study and collected data. HB and SS determined the species. SV, AP, and ST developed the idea and analysed the data. SV, AP, and ST interpreted the data. SV led the writing of the manuscript. All co-authors contributed to improve later drafts.

A.3 Publication list

List of articles published in peer-reviewed journals during the time of this thesis.

Articles considered for this thesis:

Vogel, S., Prinzing, A., Bussler, H., Müller, J., Schmidt, S. & Thorn, S. (2021). Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood. *Ecology and Evolution*, *11*(11), 6881-6888. doi: 10.1002/ece3.7535.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2021). Corrigendum: Diversity and conservation of saproxylic beetles of 42 European tree species – an experimental approach from early successional stages using branches. *Insect Conservation and Diversity*, *14*(3), 412-414. doi: 10.1111/icad.12496.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E. & Thorn, S. (2020). Diversity and conservation of saproxylic beetles of 42 European tree species – an experimental approach from early successional stages using branches. *Insect Conservation and Diversity*, *14*(1), 132-143. doi: 10.1111/icad.12442.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J, & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. *Journal of Applied Ecology*, *57*(10), 2075–2085. doi: 10.1111/1365-2664.13648.

Additional articles:

Leroy, B.M.L., Seibold, S., Moriniere, J., Bozicevic, V., Jaworek, J., Roth, N., **Vogel, S.,** Zyntynska, S., Petercord, R., Eichel, P., & Weisser, W.W. (2021). Metabarcoding of canopy arthropods reveals negative impacts of forestry insecticides on community structure across multiple taxa. *Journal of Applied Ecology*, accepted. doi: 10.1111/1365-2664.14110

Thorn, S., Seibold, S., Leverkus, A.B., Müller, J., Noss, R.F., Stork, N., **Vogel, S.**, & Lindenmayer, D.B. (2020). The living dead-acknowledging life after tree death to stop biological degradation of the world's forests. *Frontiers in Ecology and the Environment*, *18*(9), 505-512. doi: 10.1002/fee.2252.

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A.4 Curriculum vitae

Personal data

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Education

02/2017-today	PhD student, Julius-Maximilians-University Würzburg, Department of Animal Ecology and Tropical Biology
10/2014-01/2017	Master of Science (Biology), Justus-Liebig-University Gießen Thesis: "Abundance of parasitoid Hymenoptera decreases along a gradient of phylogenetic diversity of saproxylic beetle assemblages" Grade: 1.2
10/2011-10/2014	Bachelor of Science (Biology), Martin-Luther-University Halle-Wittenberg Thesis: "Untersuchungen zur Diskriminierung numerischer Informationen bei Fischen am Beispiel des Zebrabärblings (*Danio rerio*)" Grade: 1.8
08/2004-06/2011	Abitur, Julius-Spiegelberg-Gymnasium Vechelde Grade: 2.4

Professional experiences

03/2020-today	Scientific staff at the Bavarian Environment Agency, Biodiversity Centre Rhön
01/2017-today	Freelance consultant for ornithology and environmental education
08/2019-06/2020	Scientific staff at the Julius-Maximilians-University Würzburg, Department of Animal Ecology and Tropical Biology

07/2019-03/2020	Employee at the District Government of Lower Franconia, Higher Nature Conservation Authority
05/2016-10/2016	Scientific assistant at the Justus-Liebig-University Gießen, Department of Animal Ecology
03/2015-04/2015	Scientific assistant at the University of Veterinary Medicine Hannover, Institute for Terrestrial and Aquatic Wildlife Research

Grants

2018	Conference grant by the German academic exchange service
2017	Dissertation fellowship by the German Environmental Foundation

Reviewer

Since 2019	European Journal of Forest research