



Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt
Lehrstuhl für Zoologie, Arbeitsgruppe Entomologie

Drivers of saproxylic biodiversity and prospects for conservation

Jonas Hagge

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Zusammenfassung

Wälder stellen für die Menschheit wichtige Funktionen bereit. Dazu zählen unter anderem Holz als vielseitige Ressource und die Speicherung von Kohlenstoff. Zugleich leisten Wälder einen zentralen Beitrag zur Biodiversität. Weltweit haben Entwaldung und eine auf Holzproduktion optimierte Forstwirtschaft den natürlichen Charakter von Wäldern grundlegend verändert. Der Verlust an Strukturelementen natürlicher Wälder und eine dramatische Reduktion der Menge und Vielfalt von Totholz haben zum Verlust xylobionter (i.e., auf Totholz angewiesener) Arten geführt und die damit verbundenen Ökosystemfunktionen der Wiederaufbereitung von Energie und Nährstoffen in Wäldern beeinträchtigt. Die häufiger werdenden und stärker ausfallenden natürlichen Störungen in Wäldern (i.e., Windwürfe, Waldbrände, Dürren) haben zudem Insekten-Kalamitäten gefördert und zu einer Verschärfung der Kontroverse zwischen Naturschutz und Forstwirtschaft geführt. Ein evidenzbasiertes Verständnis der Einflussfaktoren, welche die Biodiversität von xylobionten Organismen bestimmen, ist die Grundlage für ein zielführendes Naturschutzmanagement. Innovative Managementoptionen stellen die Grundlage für die Entwicklung von Strategien dar, die den Schutz der Biodiversität von Wäldern mit den vielfältigen Funktionen von Waldökosystemen, inklusive der Holzproduktion, verbinden.

Die Studie, die im ersten Artikel beschrieben ist, zeigt für die Buchenwälder Europas ein übereinstimmendes Muster der funktionalen Biodiversität von xylobionten Käfern und Pilzen. Dieses Muster ist durch die biogeografische Geschichte Europas, das Klima und die Landnutzung beeinflusst. Die funktionale Biodiversität verringert sich entlang des historischen Rückwanderungsverlaufs der europäischen Biozönose von Süd nach Nord und mit der Zunahme der Landnutzung auf regionaler und kontinentaler Skala. Da hingegen steigern passende klimatische Bedingungen für die Rotbuche die funktionale Biodiversität der assoziierten Xylobionten. Funktionale Filter für xylobionte Käfer und Pilze operieren dabei vor allem auf der regionalen Skala. Für den Schutz funktionaler Biodiversität sollten daher Gebiete über das gesamte Verbreitungsgebiet der Buchenwälder ausgewählt und die unterschiedlichen klimatischen Standorte mit eingeschlossen werden.

Die Studie des zweiten Artikels demonstriert das insgesamt geringe Potential für den Schutz der Biodiversität von Käfern in anthropogenen Habitaten, die für die Forstwirtschaft und Landwirtschaft optimiert sind. Die Biodiversität der Käfer nimmt in anthropogenen Habitaten mit einer gesteigerten Landnutzungsintensität ab, dies umfasst verstärkte Düngung und Pestizideinsatz, häufige maschinelle Bearbeitung und kurze Umtriebszeiten. Maisfelder

weisen im Vergleich die geringste Biodiversität auf, gefolgt von Christbaumplantagen und Fichtenplantagen. Dieses Ergebnis ist alarmierend, da weltweit 13,5 % der landwirtschaftlich bewirtschafteten Flächen mit Mais bedeckt sind und fordert daher nachhaltigere Formen der Landnutzung.

Die räumliche Verteilung von Totholz in vertikaler und horizontaler Ebene ist eine wichtige Eigenschaft von Wäldern. Ein experimenteller Ansatz im dritten Artikel zeigt, dass die vertikale Achse von Wäldern zu sich differenzierenden Artengemeinschaften xylobionter Käfer zwischen den Straten führt. Die gleiche Menge und Zusammensetzung an Totholz wies dabei eine größere Artenzahl im oberen Kronendach als nahe dem Waldboden auf. Totholzäste im Kronendach vergrößern die Diversität des Totholzangebotes in Wäldern und sollten daher für einen Schutz xylobionter Arten erhalten werden. Die besondere Bedeutung von Totholz als strukturgebendes Element am Waldboden konnte im vierten Artikel gezeigt werden. In Wirtschaftswäldern kann durch ein Belassen von Kronenmaterial bei Erntearbeiten eine physikalische Barriere erzeugt werden, die den Verbiss durch Rehwild deutlich verringert. Diesem positiven Effekt von Totholz wird in Jahren und Gebieten mit einer hohen Abundanz von Nagern entgegengewirkt, da der Verbiss von Nagern im Schutz des Totholzes stärker ausfällt.

Die Studie des fünften Artikels zeigt auf, dass die Rindenbedeckung von Totholz die Prozesse der Bildung von Artengemeinschaften und die Biodiversität von xylobionten Mikroorganismen beeinflusst. Deterministische Prozesse der Bildung von Artengemeinschaften sind dabei sowohl für Pilze als auch für Bakterien relevanter in Stämmen ohne Rinde. Der Einfluss von Rindenbedeckung auf die Biodiversität unterschied sich zwischen Bakterien und Pilzen sowie für die Prozesse der Besiedlung und Fruchtkörperbildung von Pilzen. Diese Komplexität widerspricht einem generellen positiven Effekt von Rindenbedeckung für die Biodiversität Totholz besiedelnder Mikroorganismen.

Die Studie des sechsten Artikels evaluiert mechanische Manipulation der Rinde als Maßnahme der Schädlingskontrolle des Buchdruckers (*Ips typographus* L., 1758) und in Hinblick auf den Erhalt von Biodiversität. Die streifenförmige Entrindung zeigte sich als effektive Methode, um eine Besiedlung durch *I. typograpus* von durch natürliche Störungen (i.e., Windwürfe, Dürren) geschwächte Bäume zu verhindern, sowie den Befall durch *I. typograpus* in kürzlich befallenen Bäumen zu kontrollieren. Zudem erhält die Methode des Rindenstreifens die Biodiversität auf dem natürlichen Niveau, wohingegen die ursprünglich empfohlene vollständige Entrindung die Biodiversität um 54 % verringert und höhere Kosten verursacht. Von der Öffentlichkeit wird Rindenstreifen positiver wahrgenommen als

Entrindung. Die Möglichkeit relevante Faktoren für das Management geschützter Gebiete zu vereinen spricht für die Kontrolle des Buchdruckers durch Rindenstreifen anstelle einer Flächenräumung oder vollständigen Entrindung.

Die vorliegende Arbeit umschließt Freilanderfassungen und experimentelle Ansätze, die ein vertiefendes Verständnis für Einflussfaktoren der Biodiversität von xylobionten Organismen liefern. Die Erkenntnisse reichen dabei von großskaligen biogeografischen Filtern bis hin zu Funktionen der Charakteristika von Totholz auf lokaler Skala und berücksichtigen dabei verschiedene xylobionte Taxa und Erfassungsmethoden. Basierend auf den Ergebnissen werden Empfehlungen für ein Naturschutzmanagement entwickelt und weitere Schritte für die Forschung abgeleitet.

Summary

Forests provide important functions to humans. Their wood is a multifunctional resource, including for carbon storage, but forest also maintains biodiversity. However, globally, deforestation and forest management optimized for wood production have changed the natural appearance of forests. The loss of old-growth forest structures and the dramatic reductions in the amount and diversity of dead wood are linked to the decline of saproxylic, i.e., dead-wood dependent, species and the connected forest ecosystem functions of energy and nutrient recycling. The increasing frequency and severity of natural forest disturbances, i.e., wind-throws, wildfires and droughts, promote insect outbreaks and have thus exacerbated the controversy regarding forest management strategies aimed at conservation vs. wood production. Conservation management needs an evidenced-based understanding of the drivers of biodiversity, including that of saproxylic organisms, and novel strategies in order to implement suitable strategies that combine the conservation of forest biodiversity with the multifunctionality of forest ecosystems, including wood production.

The study described in the first article of this thesis demonstrated that saproxylic beetles and fungi across European beech forests have a congruent pattern of functional biodiversity, one that is affected simultaneously by biogeographic history, climate and human land-use. Functional diversity was shown to have decreased along a historical re-colonization gradient of European biota from south to north in parallel with regional and continental increases in land-use by humans. At the same time, a climate regime suitable for European beech has promoted the functional diversity of associated saproxylic taxa. The functional filters for saproxylic beetles and fungi were shown to mainly operate on a regional scale. Consequently, the conservation of functional diversity in European beech forest must focus on a broad spatial and climatic range in order to conserve the diversity of saproxylic beetles and fungi.

The study in the second article found that anthropogenic habitats optimized for forestry and agriculture purposes discourage beetle conservation. Increasing anthropogenic impacts, i.e., fertilizer and pesticide use, the frequent operation of machinery and short crop rotation periods, promote the loss of beetle diversity. The lowest biodiversity of beetles was in maize fields, followed by Christmas tree plantations and spruce plantations. This finding is alarming because 13.5% of arable land globally is covered by maize fields and call for more sustainable forms of land use.

The distribution of dead wood, both vertically and horizontally, is a distinct feature of forests. The experiment described in the third article showed that different assembles of

saproxyllic beetles are found along the vertical axis. For the same amount and type of dead wood, the species number in the uppermost canopy was higher than that near-ground. Thus, dead branches in the canopy increase diversity of dead wood and connected biodiversity in forests and should be retained as much as possible for saproxyllic beetle conservation. The study in the fourth article evidenced the importance of dead wood as a structural feature on the forest floor. In commercial temperate forests, the retention of dead wood during logging activities creates refugia from sapling browsing by roe deer. However, in years and areas of high rodent density, this positive physical barrier of dead wood for roe deer browsing may be reduced or even completely eliminated by a higher browsing activity of rodents in the shelter of dead wood.

The study comprising the fifth article demonstrated that the bark cover of dead wood controls the assembly processes and biodiversity of saproxyllic microorganisms. Deterministic assembly processes were shown to be more relevant on trees without bark, both for fungi and for bacteria. However, the effects of bark on biodiversity patterns differ between bacteria and fungi and between the processes of fungal colonization and fructification. This complexity obscures a general positive effect of bark cover on the biodiversity of wood-inhabiting microorganisms.

The study in the sixth article evaluated the effect of mechanical bark manipulation, both for pest control of the European spruce bark beetle (*Ips typographus* L., 1758) and conservation. Bark gouging (i.e. the removal of bark only in strips) effectively prevented the infestation of trees weakened by natural disturbances (i.e., wind-throws, droughts) and allowed the control of *I. typographus* in recently infested trees. It also retained biodiversity at natural levels, whereas the originally recommended procedure of debarking decreased biodiversity by 54%, and with higher economic costs. The public rated bark-gouged trees more positively than debarked trees. The potential to combine factors relevant to the management of protected areas should promote the use of bark gouging in the control of bark beetles in protected areas instead of salvage logging and debarking.

Thus, in the form of survey studies and experimental designs, the work described in this thesis provides a deeper understanding of the drivers of saproxyllic biodiversity, ranging from large-scale biogeographic filters to the local-scale functioning of dead wood characteristics. These findings based on data obtained with different sampling methods and included a wide range of saproxyllic species groups. The results have been synthesized herein to develop a framework of recommendations for a conservation-oriented management and further research perspectives are outlined.

1. Introduction

1.1 Saproxylic biodiversity – drivers and functions

Comparable to the diversification of pollinators and herbivores with the evolution of flowering plants, the appearance of dead wood in the early Devonian forest has led to the diversification of saproxylic life, beginning at least 385 million years ago (Stokland *et al.*, 2012; Ulyshen and Šobotník, 2018). Today, woody biomass is estimated to comprise ~70% of total biomass across all taxa on Earth, thus providing a comprehensive resource and habitat for saproxylic species (Bar-On *et al.*, 2018). Although the enormous amount of energy tied up in woody material can perhaps be best appreciated by sitting beside a campfire; the transformation of this energy for use by saproxylic species is challenging (Stokland *et al.*, 2012).

Life in dead or dying trees is present in a fascinating diversity of forms all over the world. The organisms in these habitats carry out the important ecosystem function of wood decomposition and thus the recycling of energy and nutrients (Harmon *et al.*, 1986; Stokland *et al.*, 2012). In this thesis, the ecologically broad definition of saproxylic species groups given by Stokland *et al.* (2012) has been adopted: “any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees.” Among saproxylic species, fungi and arthropods are by far the most diverse groups, but bacteria, nematodes, birds, mammals, mollusks and some crustaceans also depend on dead wood as a resource or habitat (Stokland *et al.*, 2012). The total number of saproxylic species both worldwide and regionally is for the most part unknown (Stokland *et al.*, 2012). Based on data from northern Europe, the saproxylic species make up an estimated to 20–25% of all forest-dwelling species (Siitonen, 2001). The most diverse order of saproxylic invertebrates is Coleoptera, as 122 (65%) of the 187 presently recognized beetle families have at least one saproxylic member (Gimmel and Ferro, 2018). In some well-studied forest reserves in Germany, 56% of all forest-dwelling beetles are saproxylic beetles (Köhler, 2000).

Organisms depend on dead wood to fulfill many different functions, even for the same species. For saproxylic species, dead wood serves as a food resource, as shelter, as a foraging ground, as a habitat for oviposition, nesting and hibernation and as a buffer against changing or unfavorable environmental factors (Speight, 1989; Boddy *et al.*, 2008; Stokland *et al.*, 2012; Ulyshen, 2014). Conversely, most saproxylic species can be sorted

by their functional role and their trophic level in a saproxylic food web in which the decomposition of wood is the core process. Saproxylic species with an epixylic lifestyle, i.e., mosses and lichens, but also nesting vertebrates supplement their diet with nutritional sources outside this food web. Different groups of fungi (i.e., white rot, brown rot and soft rot) chemically decompose cellulose, hemicellulose and lignin directly by secreting a very wide variety of enzymes (Rayner and Boddy, 1988; Pérez *et al.*, 2002). Saproxylic invertebrates mainly promote decomposition by physical destruction, leading to reduced particle sizes and an increased surface area for the enzymatic activities of microorganisms, including fungi (Ulyshen, 2014). Invertebrate boreholes facilitate access by microorganisms and improve the aeration of the wood interior (Ulyshen, 2014). Invertebrates may also be important vectors for saproxylic microorganism, enabling their substrate-specific dispersal (Ulyshen, 2014; Seibold *et al.*, 2019). The associations between invertebrates and fungi in wood decomposition are highly diverse (Six, 2012; Kirkendall *et al.*, 2015; Ulyshen and Šobotník, 2018). Endosymbiosis with fungi and bacteria allows the digestion of wood material by the invertebrate host (Martin, 1991). Ectosymbioses are particularly frequent in fungi-farming (ambrosia) beetles, with associations ranging from mutualistic to commensal, and from facultative to obligate (Six, 2012; Kirkendall *et al.*, 2015). Predators acting at different trophic levels as well as parasites, including mycoparasites and hyperparasitoids, are two additional functional components of the highly diverse saproxylic food web (Stokland *et al.*, 2012).

Dead wood is a complex habitat offering a multitude of different niches for saproxylic biodiversity. In addition to the enormous energy base represented by woody material, niche differentiation is the main driver of the enormous species and functional diversity of saproxylic organisms (Köhler, 2000; Boddy *et al.*, 2008; Möller, 2009; Stokland *et al.*, 2012). Host tree species, wood-decay stage, the occurrence of different tree-related microhabitats and the different size classes of wood describe the possible habitat dimensions of dead wood objects, with each species utilizing only a portion of each dimension (e.g., Heilmann-Clausen and Christensen, 2004; Stokland *et al.*, 2012; Gossner *et al.*, 2016; Larrieu *et al.*, 2018). In addition, the niche space of a dead wood object is extended by the local environment and the circumstances of the woody plant's death (Müller *et al.*, 2015; Ottosson *et al.*, 2015). For example, microclimatic conditions in forest are often mediated by canopy cover, which is a major habitat filter for saproxylic beetles (Seibold, Bässler, Brandl, *et al.*, 2016); by contrast, for saproxylic fungi, microclimate is less important than host-tree identity (Krah *et al.*, 2018). The vertical and horizontal

distributions of dead wood also influence saproxylic biodiversity (Schiegg, 2000; Weiss *et al.*, 2016). For example, dead wood lying on the ground is exposed to different physical factors (i.e., moisture and temperature) than is upright dead wood at the same site (Brunet and Isacsson, 2009; Pouska *et al.*, 2016). Dead wood in the canopy layer is exposed to strong solar radiation (Parker, 1995), which may affect the species richness and community composition of saproxylic organisms.

Initial dead wood colonization processes are important and priority effects, i.e., the effect of the prior arrival of a particular species on subsequent community development, can determine the composition of later assemblages of saproxylic species (Fukami *et al.*, 2010; Hiscox *et al.*, 2015). In addition, the species pool of endophytic microorganisms present before tree death could affect colonization by saproxylic species (Song *et al.*, 2017). Early-successional saproxylic species colonizing dead wood are confronted with tree bark as the outermost layer. Bark protects living trees against physical (e.g., fire) and biological (e.g., bark beetles and microbial pathogens) influences and forms a buffer against climatic oscillations of temperature and moisture (Srivastava, 1964; Pinard and Huffman, 1997; Franceschi *et al.*, 2005; Rosell *et al.*, 2014). Bark is also more energy rich than hard wood and by mediating the moisture content of the underlying wood promotes dead wood decomposition (Dossa *et al.*, 2016, 2018; Ulyshen *et al.*, 2016). However, the mechanisms by which bark determines the assembly and biodiversity of saproxylic species are mostly unknown.

The high species and functional diversity of saproxylic organisms at a given site correlate with a high diversity of dead wood resources (Müller and Bütler, 2010). This pattern can be explained by the habitat heterogeneity hypothesis, which predicts that the number of species increases with increasing habitat heterogeneity, because an increased number of niches allows for the coexistence of a greater number of species (Simpson, 1949; MacArthur and MacArthur, 1961). However, under natural conditions, the amount of dead wood often correlates with dead wood diversity (Müller and Bütler, 2010). Therefore, as an alternative to the habitat heterogeneity hypothesis, the species energy hypothesis simply predicts a positive relationship between the amount and species richness of dead wood due to the increase in the availability of energy (Wright, 1983; Srivastava and Lawton, 2013; Schuler *et al.*, 2015). In an experimental approach aimed at separating the effects of dead wood amount and diversity for saproxylic beetles, Seibold *et al.* (2016) found support for the habitat heterogeneity hypothesis but no evidence for the species energy hypothesis. However, based on the same experimental design, another study showed that the diversity

of saproxylic fungi could not be explained by either hypothesis (Krah *et al.*, 2018). Due to direct feedback between species traits and the environment, trait-based functional diversity rather than species richness may better serve as a biodiversity measure that well reflects habitat heterogeneity and environmental gradients (Hooper *et al.*, 2005; Flynn *et al.*, 2009). Locally, the correlations between taxonomic and functional diversity for saproxylic beetles and fungi may be similarly affected by climate and local habitat factors (Thorn, Förster, *et al.*, 2018). However, similar functional analyses of saproxylic biodiversity on a continental scale for an entire forest type are lacking. The importance of such studies lies in their ability to shed light on the historical and environmental drivers of species assemblages at different scales that result in different species pools at local and regional scale (Mittelbach and Schemske, 2015; Zobel, 2016).

1.2 History and current situation of temperate forest in Europe

“Saproxylic insects and the unsustainable management of forests: a 5000-year European experiment”

Grove (2002)

Before human colonization, the biota in Europe were shaped by the biogeographical history of this region and by abiotic and biotic environmental factors (Lomolino *et al.*, 2016). Quaternary climatic oscillations between glacial and inter-glacial periods forced species to continuously migrate, seeking refugia located mainly in Mediterranean regions during cold periods and areas favorable to re-colonization in the north during warm periods (Hewitt, 2000). The lower tree species richness in Europe than in North America can partly be explained by the more pronounced glacial extinctions in Europe, due to the orientation of the continent’s mountain ranges in the east-west direction, which thus form boundaries to migration (Adams and Woodward, 1989). In the case of European beech (*Fagus sylvatica* L.), the re-colonization that began during the last glacial maximum (~20,000 years ago)—towards the north in Sweden and towards the northeast in Poland from several distinct refugia in southern Europe—is a still-ongoing process (Latalowa, 1992; Björkman, 1996; Magri, 2008). Post-glacial dispersal limitations are also evident in the patterns of plant species richness and functional diversity that characterize the understory of European beech forests, where diversity decreases with increasing distance to potential refugia (Willner *et al.*, 2009; Ordonez and Svenning, 2015). For saproxylic species dependent upon the occurrence of long-living tree species, the Quaternary legacy for the functional components of biodiversity should be even more complex, but empirical evidence is lacking.

Forests ecosystems in lowland temperate Europe were probably the dominant ecosystem in Europe before the onset of significant human influence, ~5,000 years ago (Grove, 2002; Svenning, 2002; Mitchell, 2005; Leuschner and Ellenberg, 2017). Primary forest is defined by the absence of habitat fragmentation due to anthropogenic disturbance and by the presence of habitat continuity, all forms of natural disturbance, a high amount and diversity of dead wood and the natural tree species community of the climatic domain (Lachat and Müller, 2018). For European beech forests, these factors allow for dead wood accumulations of up to 550 m³ per hectare (Christensen *et al.*, 2005). The advent of human settlements and agriculture led to the progressive and dramatic deforestation of Europe (Grove, 2002; Kaplan *et al.*, 2009; Leuschner and Ellenberg, 2017). This process was accelerated by the hyperexponential growth of the human population and the demands for resources that fueled the Industrial Revolution, including firewood, timber for construction, as well as open land for settlement and factory construction and for agriculture (Varfolomeyev and Gurevich, 2001; Grove, 2002; Kaplan *et al.*, 2009). The remaining forest areas were mainly located on pure soils and areas of rough topography, which discouraged their use as pastures and arable land (Kaplan *et al.*, 2009). Due to the enormous need for wood, pressure on the remaining forest was high, such that the loss of old-growth forest structures and reductions in the amount and diversity of dead wood changed the natural appearance of the forest (Siitonen, 2001; Grove, 2002; Lindenmayer, Laurance, *et al.*, 2012). With the introduction of modern forestry practices, beginning in the late 18th century, indigenous broad-leaved tree species were gradually replaced by fast-growing conifers; the natural growing stock was converted to homogenized, even-aged shaded stands and moribund and old trees as well as dead wood were removed (Grove, 2002). Studies comparing primary and managed forests have clearly documented a loss of species richness and abundance accompanied by a changed species composition (reviewed in, Grove, 2002; Paillet *et al.*, 2010; Lachat and Müller, 2018). Saprophytic species, which rely on the continuity of primeval habitat features and the large-scale availability of dead wood are particularly vulnerable to the negative impacts of forest management (Blaschke *et al.*, 2009; Eckelt *et al.*, 2018). Estimates of the amount of dead wood that has been lost compared to old-growth forests in Central Europe are complicated by the lack of old-growth forests as a reference. Today, the amount of dead wood in boreal and temperate forests has been reduced to an average of ~10 m³ per hectare across all forest types (European Environment Agency, 2015) and 21 m³ per hectare in Germany (BWI, 2012). Assuming natural amounts of dead wood of 60–90 m³ per hectare in boreal European

forests (Siitonen, 2001) and a median of 157 m³ per hectare in temperate European old-growth forests (Burrascano *et al.*, 2013), the remaining amount of dead wood is only 10–20% of the natural amount, which is far below the derived habitat thresholds needed to maintain saproxylic biodiversity (Müller and Büttler, 2010; Müller *et al.*, 2010).

With the dramatic reductions in the amount and diversity of dead wood, habitat transformation and loss by fragmentation, the intensive management of natural disturbances and a forest structure optimized for wood production, saproxylic organisms have become a highly threatened species group in European forests and beyond (Speight, 1989; Grove, 2002; Davies *et al.*, 2008; Stokland *et al.*, 2012). The European Red List of saproxylic beetles evaluates only a small subset of saproxylic beetle species (Nieto and Alexander, 2010). Of the 431 recognized species, 48% are considered as unthreatened (least concern) in Europe, 11% are threatened, 13% are near threatened, and for 28% the data are insufficient for classification (Nieto and Alexander, 2010). In the comprehensive Red List of the saproxylic beetle species of Germany, 52% of the 1392 recognized species are unthreatened (least concern), 22% are threatened, 18% are threatened to an unknown extent, are near threatened or extremely rare, and for 8% the data are insufficient for classification (Schmidl and Büche, 2019). A model of the extinction risk of saproxylic beetle species in Europe revealed a higher extinction risk for lowland and large species as well as for species that rely on wood of large diameter, broad-leaved trees or open canopy (Seibold *et al.*, 2015). These results well-reflect the intensification of forestry practices in European forests over a period of several centuries, during which time natural broad-leaved forests have been converted to dense conifer-dominated forests and old growth trees and dead wood have been lost (Grove, 2002).

Human impact on forest ecosystems is reflected not only by deforestation and forest management optimized for wood production, but also by management strategies that have altered the densities of large mammal species. Human management aimed at the extirpation of large carnivores (Chapron *et al.*, 2014) together with the strict regulation of culling (Apollonio *et al.*, 2010) has led to an overabundance of cervids (Putman, 1992). In Europe, roe deer are distributed across most of the continent (Andersen *et al.*, 1998), inhabiting agricultural landscapes as well as forests, where they are often found at high population densities. In the forest understory, herbivory by roe deer has been shown to adversely impact forest regrowth and to alter the composition of forest plants (Fuller and Gill, 2001; Moser and Schütz, 2006; Boulanger *et al.*, 2018). Survey studies suggest that dead wood on the forest floor can serve as a natural physical barrier to large browsers and thus play a

positive role in forest regeneration (Kupferschmid and Bugmann, 2005; de Chantal and Granström, 2007). Shelters created by wind-blown trees provided refugia from browsing (Long *et al.*, 1998). However, evidence for a general positive effect of dead wood on the forest floor, and specifically for a reduction in browsing pressure on the saplings in commercial forests in Europe, is missing.

1.3 Natural disturbances and forest pest species

“A small minority of saproxylic species such as some bark beetles can compete successfully with humans and are therefore termed pests.”

Grove (2002)

Natural disturbances, such as wind-throws, wildfires, droughts and insect outbreaks, are a fundamental element of forest dynamics (Turner, 2010). Disturbances disrupt the structure, composition and function of ecosystems and change both the physical environment and resource availability (Pickett and White, 1985; Seidl *et al.*, 2017). They also create landscape heterogeneity and thus have an overall positive influence on biodiversity (Beudert *et al.*, 2015; Thom and Seidl, 2016). However, disturbances generally have a negative impact on ecosystem services, such as carbon storage, timber and primary production (Thom and Seidl, 2016). In Europe, disturbances over the period 1950–2000 caused damage to an annual average of 35 million m³ wood, ~8.1% of the total fellings and ~0.15% of the total volume of growing stock (Schelhaas *et al.*, 2003). Forest management thus aims at minimizing the impacts of disturbances (Thom and Seidl, 2016). However, forest practices aimed at increasing growing stocks and promoting even-aged monocultures, result in forests that are particularly vulnerable to disturbance (Bengtsson *et al.*, 2000; Schelhaas *et al.*, 2003). Moreover, the double hits of climate change and forest change have increased the frequency and severity of disturbances in Europe over the last few decades, with further increases predicted (Seidl *et al.*, 2011, 2014, 2017).

Links between abiotic (e.g., wind, drought, fire) and biotic (e.g., insects) disturbances are particularly strong. In one study, > 40% of insect disturbances could be directly associated with previous abiotic disturbances (Seidl *et al.*, 2017). An important source of disturbance in Eurasia is the European spruce bark beetle (*Ips typographus* L., 1758), considered to be a major insect pest. In its main host-tree species, Norway spruce (*Picea abies* (L.) H. Karst.), bark beetle populations erupt after drought and windstorms (Seidl *et al.*, 2016). Bark beetle damage, mainly by *I. typographus*, in Europe affected 14.5 million m³ of wood annually during the first decade of the 21st century, which corresponds

to an increase of > 600% compared to the previous three decades (Seidl *et al.*, 2014). A further increase of bark beetle damage, to 17.9 million m³ of wood annually, is predicted for the period 2021–2030 (Seidl *et al.*, 2014). However, *I. typographus* is also a keystone forest species that promotes biodiversity (Müller, Bußler, Goßner, *et al.*, 2008; Beudert *et al.*, 2015) and shares its habitat with several hundreds of other species, many of which are endangered (Lehnert *et al.*, 2013; Thorn, Bässler, Bußler, *et al.*, 2016; Kazartsev *et al.*, 2018).

Extensive outbreaks of bark beetles are one reason for post-disturbance salvage logging activities, in which the aims are to eliminate potential breeding habitats of bark beetles from forests and to remove colonized bark beetle trees, thus preventing more extensive outbreaks (Wermelinger, 2004; Lindenmayer *et al.*, 2008; Thorn, Bässler, *et al.*, 2018). Salvage logging is also conducted to capture the economic value of dead or damaged trees (Prestemon *et al.*, 2006), reduce potential fuels available for subsequent fires (Sessions *et al.*, 2004), but also to “tidy up” the forest so that its appearance is in line with social conceptions of nature (Flint *et al.*, 2009). However, in protected areas worldwide, salvage logging for pest control has become one main argument for interventions resulting in the removal of trees damaged by disturbances (Müller *et al.*, 2018). Salvage logging reduces the amount and diversity of dead wood produced by the energy pulses of natural disturbances. The removal of tree trunks reduces dead wood by amounts of 70–90% (Priewasser *et al.*, 2013; Thorn, Bässler, Bernhardt-Römermann, *et al.*, 2016) and thus, not surprisingly, reduces the diversity of saproxylic species (Thorn, Bässler, *et al.*, 2018) and changes the dominant species-assembly mechanism (Thorn, Bässler, Bernhardt-Römermann, *et al.*, 2016). By contrast, species of taxa that are commonly associated with open habitats, such as carabids and epigeal spiders, respond positively to salvage logging (Thorn, Bässler, *et al.*, 2018). Alternatives to salvage logging are needed in forest areas set aside for biodiversity conservation or managed by ecologically sustainable forest management practices (see Section 1.4), if non-intervention strategies are not an option and pest control is desired or mandatory (Thorn, Bässler, *et al.*, 2018). One on-site method of pest control that has been promoted, particularly for protected areas, is mechanical bark removal (Wermelinger, 2004; Kausrud *et al.*, 2012). However, the complete removal of bark has profoundly negative effects on biodiversity, resulting in a loss of around one-third of the species in the affected tree (Thorn, Bässler, Bußler, *et al.*, 2016). Hence, bark scratching, which removes only enough of the bark to make the tree uninhabitable for *I. typographus* and has no collateral damage for non-target biodiversity, has been promoted

as an alternative (Thorn, Bässler, Bußler, *et al.*, 2016). Nevertheless, whether bark scratching is effective only as a preventative measure (i.e., before *I. typographus* colonizes weakened trees) or also provides an effective means to control *I. typographus* in recently infested trees is unclear. Further questions are how bark scratching can be standardized to handle larger outbreaks and how bark-scratched trees are perceived by human visitors of protected areas.

1.4 Dimensions and challenges to conservation in European forests

Forest ecosystems are multifunctional, with multiple stakeholders whose demands and objectives differ. The ecosystem services delivered by forest ecosystems that contribute to human well-being are comprehensive (i.e., provisioning, regulating, cultural and supporting ecosystem services) and include the provisioning of timber (MEA, 2005). Provisioning of timber together with the primary production function of forests has long dominated forest management decision-making in Europe (Grove, 2002). Given that the supporting function of nutrient cycling in forest ecosystems is closely connected to saproxylic biodiversity (Stokland *et al.*, 2012), whether forests should mainly be managed for wood production or whether wood production should be seen as an integrative function of forest management has been a topic of debate (Lindenmayer and Franklin, 2002; Puettmann *et al.*, 2008).

Forest biodiversity conservation strategies can be classified in terms of their aim, which may be reservation, retention or restoration (Brunet *et al.*, 2010). In Europe, forests with no traces of intervention are extremely rare, and only 0.2% of the deciduous forests in Central Europe are considered to be in a natural state (Hannah *et al.*, 1995). However, for species dependent on forests with an old-growth structure and habitat continuity, these sites are the last refugia, and their reservation, including of the surrounding buffers, is therefore of high priority (Lachat and Müller, 2018). In their evaluation of European forests, Sabatini *et al.* (2018) found that only 0.7% of the forest area consisted of naturally regenerated forests containing native species, with no clearly visible indications of human activities and ecological processes that were not significantly disturbed. These remaining primary forest patches represent a valuable reference for managed forests (Lachat and Müller, 2018) but only 46% are strictly protected (Sabatini *et al.*, 2018).

In contrast to these small patches of protected forest, ~93% of the forests in Europe are under different forest management intensities but are candidates for an integrative conservation strategy of retention (Lindenmayer, Franklin, *et al.*, 2012). Ecologically

sustainable forest management is defined as “forest management that perpetuates ecosystem integrity while providing wood and non-wood values; where ecosystem integrity means the maintenance of forest structural complexity, species diversity and composition, and ecological processes and functions within the bounds of normal disturbance regimes” (Lindenmayer, Franklin, *et al.*, 2012). A case study in European beech forests found that the implementation of ecologically sustainable forest management according to a retention approach can lead to an increase in the amount of dead wood of 30 m³ per hectare during a 10-year period, from 19 m³ per hectare to 59 m³ per hectare (Doerfler *et al.*, 2017; Roth *et al.*, 2018). The diversity of saproxylic beetles and fungi increased in response to this change in forest management, reaching the same levels as in forest reserves in the same area. The species composition of saproxylic beetles also matched that of the reserves, although the species composition of saproxylic fungi continued to differ (Doerfler *et al.*, 2018; Roth *et al.*, 2018). The forest conservation strategy with the highest level of interference is the active restoration of forest ecosystems, in which the recovery of an ecosystem that has been degraded, damaged or destroyed, thus losing its natural structure, dynamics or functioning over large areas, is actively assisted (Hobbs *et al.*, 2011). For example, restoration by the controlled and planned use of fire had positive results for saproxylic biodiversity in Fennoscandia, where clear-cutting had resulted in degraded forests with dead wood in amounts of < 3 m³ per hectare (Vanha-Majamaa *et al.*, 2007; Kouki *et al.*, 2012).

Conservation of forest biodiversity refers to the genetic diversity of populations, species diversity and to the diversity of different ecosystems and their natural processes (CBD, 2010). A focus on one or the other of these different forms of biodiversity can influence the effects of different conservation strategies (Groom *et al.*, 2012). Conservation strategies may also differ between taxonomic and functional groups and there is a general need for the adequate consideration of invertebrates (Schuldt and Assmann, 2010). The impact of forest conservation is also a matter of scale, and the most obvious demands on a local scale may nonetheless be neglected if the focus is on the regional scale, and vice versa (Boyd *et al.*, 2008). Different points of view depending on the spatial scale of management also describe political decision-making levels, which range from local to federal to trans-national (Hein *et al.*, 2006).

Moreover, public perception of conservation management more often reflects political decision-making rather than ecological evidence (Burstein, 2011; Groom *et al.*, 2012). A good example is the acceptance of natural disturbances and their management

(Müller and Job, 2009). For instance, residents living near national parks have a negative attitude towards tree-killing bark beetles (McFarlane *et al.*, 2012), whereas national park visitors are more likely to have a neutral attitude (Müller and Job, 2009). Human perceptions of forests affected by natural disturbances are influenced by education and by environmental worldviews, but also by the degree of personal affinity to the national park where the natural disturbance took place (Müller and Job, 2009). This is also true for ecological restorations emulating disturbances (Long, 2009).

2 Main objectives

The main objective of the research performed for this thesis was an improved understanding of the structures and processes that drive the biodiversity of different saproxylic species groups in temperate forests. Such studies are needed for more effective conservation measures (Figure 1). A specific aim was to determine the impacts of biogeographical history, climate and land-use intensity at different scales on saproxylic biodiversity in European beech forests. In this context, the impact on beetle biodiversity conservation of anthropogenic habitats optimized for forestry and agriculture was examined. In addition, to obtain ecological evidence supporting conservation-oriented management in forests, the value of dead wood as a key structure and habitat in forest ecosystems was evaluated in four experiments (Figure 1). Dead wood was considered as a resource with different properties focusing on vertical distribution and bark coverage, as a physical structure on the forest floor and as a potential breeding habitat of tree-killing insect species. With respect to the latter, and to pest control of the European spruce bark beetle in particular, a holistic approach comprising different mechanical bark treatments was assessed for its ability to incorporate pest control, biodiversity conservation, public perceptions and economic costs.

The specific sub-goals of this thesis were:

1. To identify the patterns and processes underlying the functional diversity of saproxylic beetles and fungi in European beech forests and distinguish among biogeographical, climatic and land-use effects; to reveal the elements that must be taken into account in conservation planning and testing for congruent diversity patterns among distinct species groups (Article I).
2. To compare the conservation value of anthropogenic habitats optimized for forestry and agriculture, focusing on spruce plantations, Christmas tree plantations and maize fields (Article II).
3. To analyze the vertical gradient in forest ecosystems, from the near-ground to the upper canopy, to evaluate the importance of dead branches in the canopy for saproxylic beetle conservation (Article III).
4. To identify the potential of dead wood on the forest floor as a physical barrier that excludes large herbivores and thus prevents their browsing of saplings (Article IV).

5. To determine the effect of the bark coverage of dead trees in the assembly processes and biodiversity of microbial decomposers (Article V).
6. To develop an integrative approach to bark beetle management that incorporates all relevant management necessities of the protected areas; to evaluate the effect of mechanical pest control measures in reducing the populations of insect pests while maintaining non-target biodiversity, retaining the high recreational value of the forest and keeping the economic costs low (Article VI).

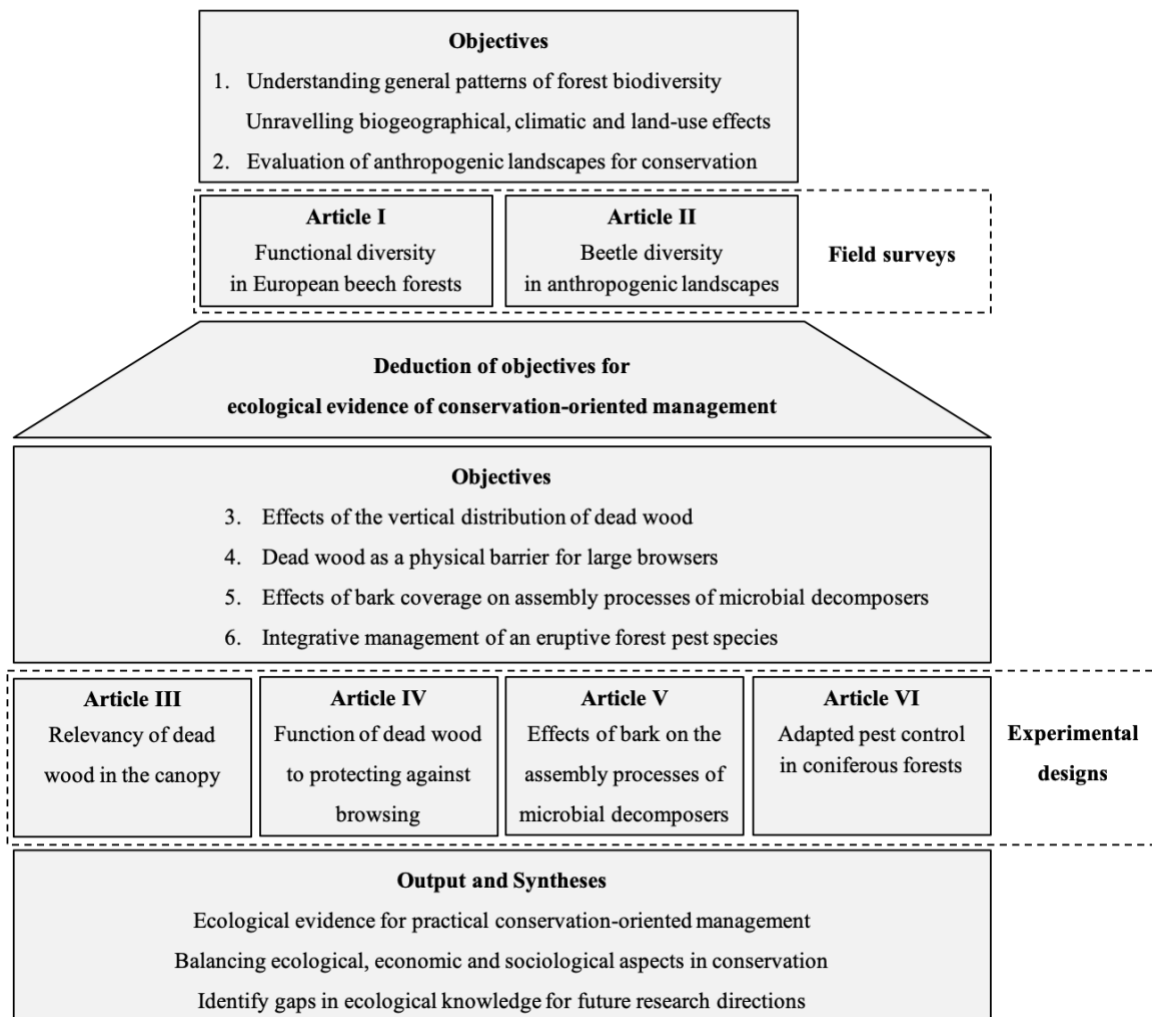


Figure 1: Conceptual framework of this thesis. The results of two different field surveys are analyzed to better understand the topics in the first and second objectives (Articles I and II). Objectives 3–6 then focus on the properties of dead wood in terms of its ecosystem functions and conservation prospects, investigated in four experiments (Articles III–VI).

3 Methods

This thesis combines analyzes from two different field surveys, both aimed at understanding the patterns and processes of biodiversity (Articles I–II), together with four experiments that focused on the different features of dead wood with respect to biodiversity and ecosystem functioning (Articles III–VI). The spatial extent of the studies in this thesis ranged from a macroecological perspective to the landscape scale to stand level to a single dead-wood object. The studied species groups included saproxylic beetles, fungi and bacteria and, as browsing agents of saplings in the shelter of dead wood, roe deer and rodents. Depending on the objective of the study, beetles were sampled with flight-interception traps, Malaise traps, emergence traps or by the rearing of baited dead wood objects. Fungi were sampled by fruit body surveys or together with bacteria by molecular methods. For Article VI, an online questionnaire was designed to quantify public perceptions of undamaged, gouged and debarked logs for bark beetle management. Statistical analyses consisted of linear mixed-effects models, ordinal regression models, analyses of community composition and null modeling approaches for determinations of trait-based functional diversity and phylogenetic turnover.

3.1 Species surveys and experimental designs

3.1.1 Saproxylic diversity of beetles and fungi in European beech forests

The functional diversity of saproxylic beetles and fungi in European beech forests was investigated using standardized survey data. For saproxylic beetles, the survey was based on data obtained during one full vegetation period from 1,404 flight-interception traps nested in 105 beech-dominated managed and protected forest areas in 10 countries. For saproxylic fungi, the survey data comprised fruiting body surveys of 1,814 fallen beech logs nested in 53 different beech-dominated forest areas in 12 countries (Figure 2). Here, region is defined as the forest area sampled by the sum of the traps or logs within a district forest site, and the regional species pool as the total species present within the traps or logs of one forest area. Local communities represent all species sampled per trap or log. The sampling procedures for beetles (mobile taxon) and fungi (sessile taxon) differed, consisting of passive continuously collecting traps and active object-oriented sampling, respectively. The sampling localities of the two taxa also differed (Figure 2). Two

taxonomically and geographically independent datasets representing two replicates, which were analyzed to understand assembly processes in European beech forests.

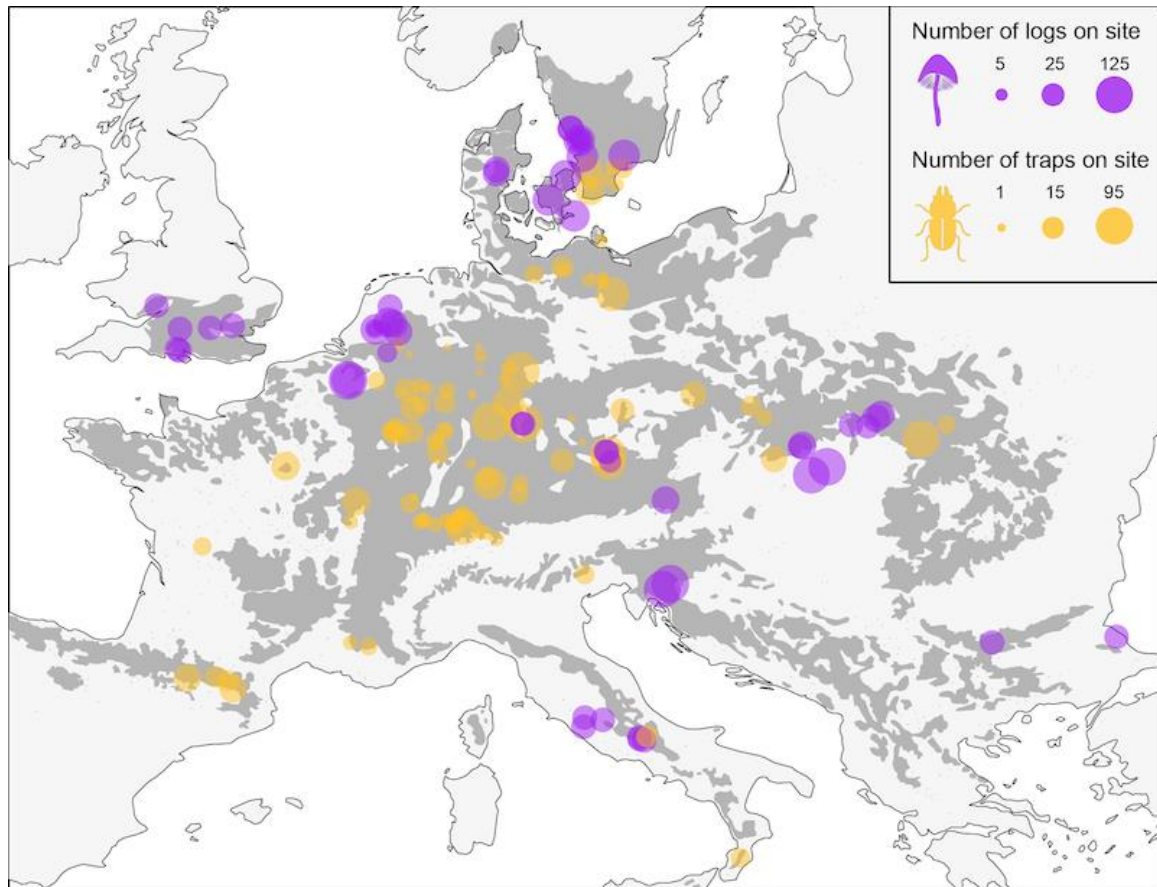


Figure 2: Map of Europe showing the study area and sampling locations used to obtain saproxylic assemblage data. The occurrence of European beech, including natural and naturalized stands, is shown in gray (EUFORGEN). Purple dots indicate the sampling locations for saproxylic fungi and yellow dots those for saproxylic beetles. The dot size refers to the number of samples of local communities obtained within each regional forest area.

3.1.2 Beetle diversity in anthropogenic landscapes

To compare the potential of three different anthropogenic landscapes in the conservation of beetle biodiversity, spruce plantations, Christmas tree plantations and maize fields were surveyed using Malaise traps. Beetles were sampled in two regions of southern Germany. In each one, four sites were selected, each consisting of three plots: one in a spruce plantation, one in a Christmas tree plantation and one in a maize field, for a total of 24 plots. The Malaise traps, designed by Prof. Bartak (bioform, Nuremberg, Germany), were 270 cm long, 100 cm wide and 170 cm high. One trap was installed per study site, at a

distance of 10 m from the field or plantation edge and parallel to the rows of planting. The traps were left on-site from June to the end of August according to the growing period of maize (silage maize was cut in the first field in late August). Beetle specimens were identified to the species level by Andreas Weigel (Wernburg, Germany) and Herbert Fuchs (Munich, Germany).

3.1.3 Vertical dead wood experiment

The aim of this experiment was to analyze the vertical stratification of saproxylic beetles from the near-floor to the upper and sun-exposed canopy of the forest. The experiment was conducted at ten stands in mature montane mixed forests located in the Bavarian Forest National Park. The stands were dominated by Norway spruce (*P. abies*), European beech (*F. sylvatica*) and silver fir (*Abies alba* Mill.). In each stand, the largest fir tree ranging above the surrounding trees was selected as a living pole. Arborists cut off the top of these trees at a diameter of 12 cm and at the top attached an aluminum arm with a rope for pulling up loads. Three bundles of freshly cut branches were placed in each tree and exposed for a full growing period, from late March to September, to allow the saproxylic beetles to colonize the dead wood. The first bundle was attached to the tree trunk 1 m above ground, the second was placed in the mid-canopy in the shade and the third immediately below the aluminum arm, fully exposed to the sun. The dead wood bundles were created from living branches without signs of insect or fungal activity that had been cut from the crown of spruce, fir and beech trees freshly felled near the study sites. Each bundle consisted of five thin (1–2 cm diameter) and three thick (5–7 cm diameter) 50-cm branches cut from each of the three tree species (24 branches per bundle). The bundles were retrieved from the trees in September and placed in a non-transparent PVC barrel (50 cm diameter and 90 cm length) for 3 years. During that time, the barrels, which had an opening covered by a fine mesh to allow air circulation, stood at ambient temperature under a roof, where they were shaded and protected from overheating. A transparent collecting jar filled with ethanol was mounted on each barrel to collect and preserve emerging beetles attracted to the light. All of the collected beetles were sorted and identified to the species level by Boris Büche (Berlin, Germany).

3.1.4 Browsing experiment

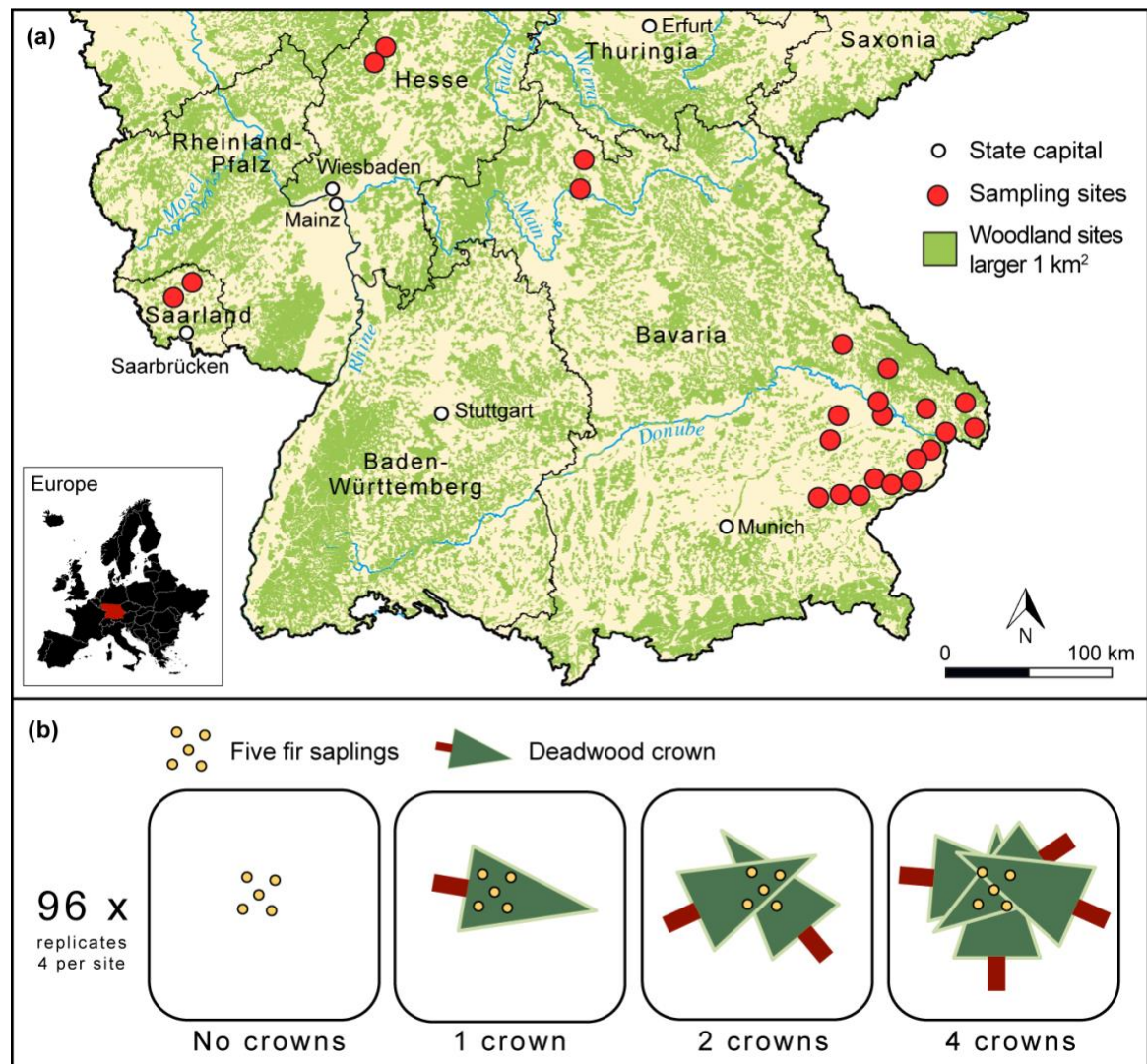


Figure 3: (a) Distribution of the study sites of the browsing experiment in southern Germany. Each site contained four replicates of the four treatments. (b) The impact of an increasingly dense physical barrier comprising dead wood crowns on roe deer and rodent browsing was tested by comparing the effects of no crowns, with 1 crown, 2 crowns and 4 crowns. Five fir saplings were planted at the center of each plot, which in the case of the three dead wood treatments were thus located within the shelter of the crown(s).

The aim of this experiment was to determine whether the addition of dead wood on the forest floor reduced browsing pressure on saplings in commercial forests in Europe. The field experiment was set up in managed temperate forests of Central Europe, at 24 sites in southern Germany (Figure 3a). Physical barriers of increasing density were established using an increasing number of tree crowns (average length: 7 m) obtained from logging activities. Four treatments, consisting of no crowns, one crown, two crowns and four

crowns, were arranged on the plots as a pile using a skidder or horses. Each of the 24 study sites contained four experimental replicates, for a total of 96 replicates and 384 experimental plots. Five silver fir (*A. alba*) saplings of similar size (30-40 cm) were obtained from tree nurseries and planted in the center of each plot. This type of sapling, both the species and its high quality due to its nursery origin, is extremely palatable to roe deer and was therefore suitable bait to examine the effect of dead wood on plot accessibility (Odermatt, 1999). The saplings were planted in a square, with one sapling at each of the four corners and one in the center (Figure 3b). For the treatments that included dead wood crowns, the saplings were planted in the shelter formed by the crowns. Nine of the study sites were in broadleaf forests, in which case the crowns were from broadleaf trees, and 15 were in coniferous forests, where the crowns were from coniferous trees. The experiment was established in autumn, between September and October (11 sites in 2016 and 13 sites in 2017), and browsing was measured the following spring, in April.

Browsing was evaluated on 1692 of the 1920 planted saplings (88%), because some saplings did not become established and others had been pulled out or could no longer be found. Saplings were counted as browsed if the terminal shoot showed traces of browsing. The considered browsing agents were roe deer, hares and rodents, identified according to the species-specific browsing traces described by Suchant et al. (2012). Red deer could be precluded as a browsing agent at the study sites because their exclusion from these areas is ensured by strict hunting-based management. If the browsing traces could not be attributed to a particular group of herbivores, the browsing agent was noted as “unknown.” Browsing intensity on the saplings, assessed for roe deer and for rodents, was determined by counting all browsed shoots and all shoots of the sapling without browsing traces, including the terminal shoot.

3.1.5 Bark removal experiment

This experiment analyzed the effect of bark coverage on assembly processes and the biodiversity of microbial decomposers in dead trees. It was conducted as part of a larger experiment investigating the effects of mechanical bark removal on biodiversity, conducted in the Bavarian Forest National Park (for details of the experimental design, see Thorn, Bässler, Bußler, *et al.*, 2016). To focus on the natural microbial community involved in decomposition Norway spruce (*P. abies*) was selected, as it is the naturally dominant tree species in this area and its decaying bark layer hosts a rich microbial fauna (Kazartsev *et al.*, 2018). Twelve study sites were established, with three vital mature spruce trees without

any bark injury selected at each one. At each site, one tree (control) was left with its bark completely intact; another was completely debarked by fully removing the bark and phloem using a debarking device mounted on a conventional chainsaw and another was partially debarked using a bark-scratching device, also mounted on a conventional chainsaw, that disrupted the bark and phloem approximately every 3 cm and thus removed ~20% of the bark.

In this study, as in other studies of microbial biodiversity in a particular environment, molecular approaches were used that identify operational taxonomic units (OTUs) [e.g., Caron *et al.*, 2009; Yoccoz *et al.*, 2012; Hoppe *et al.*, 2016]. The felled trees were sampled 1.5 years after their death, by full vertical cross-section drilling using a 0.8 cm × 30 cm auger bit and, for the partly debarked and control trees, including the bark layers (Purahong *et al.*, 2014; Hoppe *et al.*, 2016). In each felled tree, five cores regularly distributed over the length of the tree were drilled, pooling the sawdust of each tree in one sample. Each wood sample was homogenized and ground to a fine powder using liquid nitrogen and a swing mill (Retsch, Haan, Germany). Total community DNA was isolated from 0.25 g of each homogenized wood sample using the ZR Soil Microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA) according to the manufacturer's protocol. Fungal ITS2 regions were amplified using a mixture of primers P7-3N-fITS7 and P7-4N-fITS7 (*forward*) and P5-5N-ITS4 and P5-6N-ITS4 (*reverse*), which were modified from primers fITS7 and ITS4 as described in Ihrmark *et al.* (2012). Bacterial 16S rRNA genes were amplified using a mixture of the primer pairs P5-8N-515F and P5-7N-515F (*forward*) and P7-2N-806r and P7-1N-806r (*reverse*), as modified by Caporaso *et al.* (2012). The resulting PCR products were sequenced on an Illumina MiSeq system at the Deep Sequencing Group of the Technische Universität Dresden.

Raw data (FASTQ files) were processed using Geneious R9 software (Kearse *et al.*, 2012) and sequences were clustered into OTUs for fungi and bacteria using CD-HIT-EST and based on a consensus of 97% (Huang *et al.*, 2010). For the taxonomic annotation of the fungal and bacterial sequence data, representative sequences of the OTUs were blasted in SEED 2.1 (Větrovský and Baldrian, 2013) using Megablast against the NCBI nt database. Taxonomic classifications were checked using UNITE (Abarenkov *et al.*, 2010) and the NCBI GenBank. To build a subset of fungal OTUs known to be involved in wood decomposition, taxonomically identified fungal OTUs were classified based on the information from FUNGuild (Nguyen *et al.*, 2016).

3.1.6 Bark gouging experiment

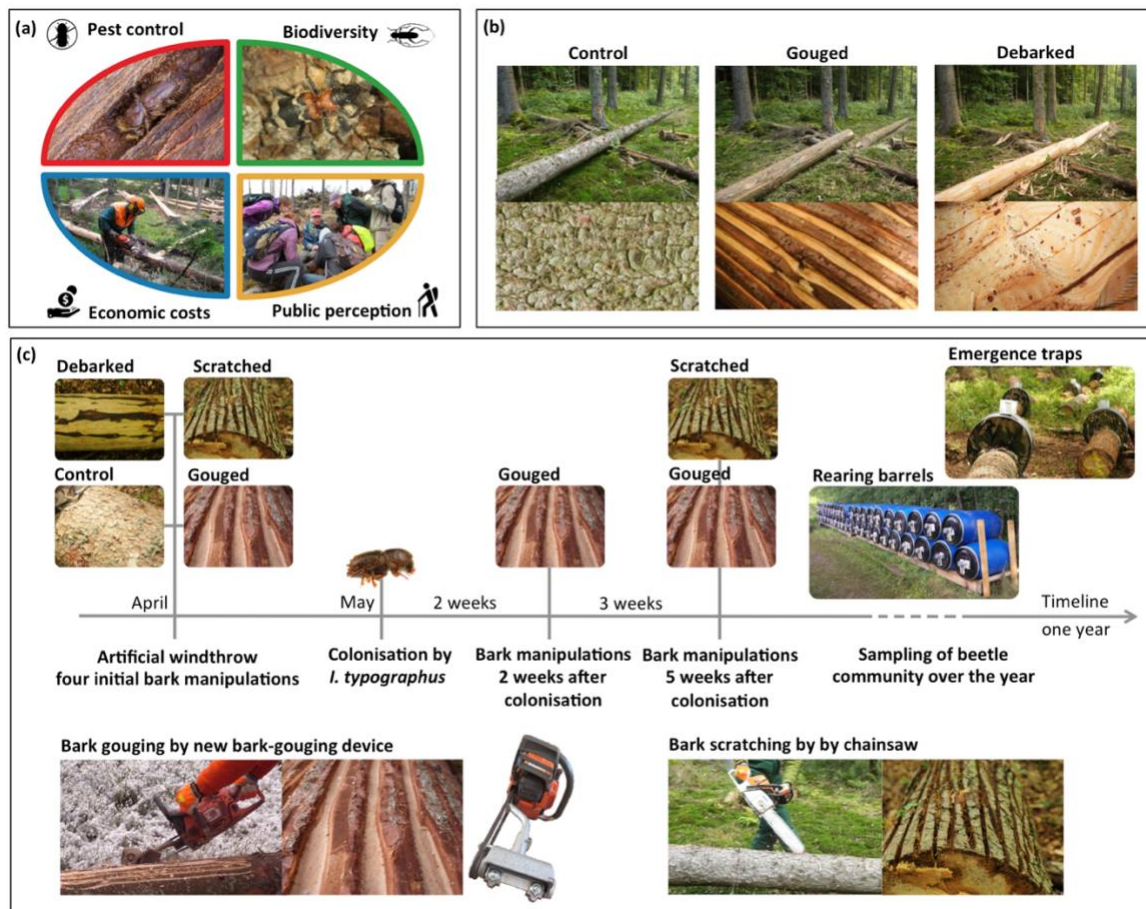


Figure 4: (a) Factors relevant to the management of protected areas. (b) Undamaged, gouged and debarked logs. The scenery photographs at the top were used in the public perception questionnaire. (c) The timeline of experiment, showing the methods used in the bark gouging experiment.

This experiment design aimed to test the potential of a newly developed device for mechanical bark gouging to reduce populations of insect pests while maintaining non-target biodiversity, retaining the high recreational value of the affected forest and keeping economic costs low. This experiment differed from the bark removal experiment described in Section 3.1.5. The experiment was conducted in the Bavarian Forest National Park, which during the last three decades has been heavily affected by outbreaks of the European spruce bark beetle (*I. typographus*) and by windstorms (Thorn *et al.*, 2017). To simulate wind-thrown trees, 24 healthy mature Norway spruce trees were felled that had no traces of *I. typographus* colonization, similar physical attributes and a diameter at breast height (1.3 m) of $37 \text{ cm} \pm 3 \text{ cm}$. Tree trunks were cut into 42 logs 5 m in length and with a mean

diameter of 31 cm \pm 3 cm. The logs were then scattered over an area of 4 ha, thereby simulating a small wind throw, in the northern part of the Bavarian Forest National Park.

The effect of a nonintervention (benign-neglect) strategy, as the control, was compared with that of debarking, scratching and gouging. Either the logs were completely debarked using a debarking device (EDER Maschinenbau GmbH, Wolfenbüttel, Lower Saxony, Germany) mounted on a conventional chain saw or the bark on the logs was scratched or gouged. For the latter two methods, the bark was either scratched every 2–3 cm using the front part of the blade of a light-weight chain saw (Stihl MS260, Stuttgart, Germany) (Figure 4c) or, gouged with a newly developed mechanical bark-gouging device (German Utility Model DE 20 2018 101 049.2). The device, which consists of two groups of four parallel V-shaped teeth with a flat front edge, was used to disrupt the phloem of the bark every 16 mm, creating patches with a width of 14 mm and a depth of 9 mm (Figure 4c). To test the efficacy of debarking in preventive pest control, i.e., before colonization by *I. typographus*, 24 logs were randomly selected directly after felling and grouped in four groups, control (bark left undamaged), debarked, scratched, and gouged, with six logs in each group. To evaluate pest control after colonization had begun, six logs were gouged 2 weeks after *I. typographus* colonization, and, six logs were scratched and six were gouged 5 weeks after colonization (Figure 4c).

Starting 5 weeks after the first colonization of the logs by *I. typographus*, arthropods were collected with both emergence traps and rearing barrels for over 1 year, to cover all potential generations of *I. typographus* (see the time line of the experiment in Figure 4c). All sampled beetle specimens were identified to the species level by Alexander Szallies (Reutlingen, Baden-Württemberg, Germany). For the evaluation of economic costs of different mechanical bark treatments, the time was measured needed to complete debarking, scratching, and gouging of 12 logs of freshly felled trees each by four professional forestry workers, who are familiar with the handling of the devices. The time needed was standardized by tree volume. To quantify the public perception of undamaged, gouged, and debarked logs, standardized photographs were taken of the same scenery by first felling a spruce tree, then gouging the bark of the tree and finally debarking the same tree (Figure 4b). The photographs were used in an online questionnaire, which was completed by a representative sample consisting of 1,008 participants in Germany. The questionnaire stated “Imagine you are on a hike in a national park. You notice a tree trunk close to the trail. It looks like one of the logs in the photos. Please score each photo according to how positive or negative you perceive the appearance of each log.” This

procedure resulted in integer response scores ranging from 1 (very negative perception) to 5 (very positive perception) for each photograph.

3.2 Measures of species dissimilarity

3.2.1 Functional traits and categories of saproxylic species

Table 1: Traits and categories of saproxylic beetles and fungi evaluated in Articles of this thesis.

	Trait	Definition	Source	Article
Beetles	Body size	Mean body length of the beetle in dorsal view (mm)	Freude <i>et al.</i> , 1983; Gossner <i>et al.</i> , 2013; Seibold <i>et al.</i> , 2015	I, III
	Wing load	Body mass divided by wing area	This thesis	III
	Wing aspect ratio	Wing length divided by wing width	This thesis	III
	Saproxylic	Yes/no	Schmidl and Bussler, 2004	I, II
	Decay niche	Preferred decay stage (fresh = 1 to decomposed = 5)	Möller, 2009; Gossner <i>et al.</i> , 2013; Seibold <i>et al.</i> , 2015	I
	Wood diameter niche	Preferred dead-wood diameter (small = 1 to large = 4)	Möller, 2009; Gossner <i>et al.</i> , 2013; Seibold <i>et al.</i> , 2015	I
	Host tree preference	Broad-leaved, conifer, both	Freude <i>et al.</i> , 1983; Köhler, 2000	I
	Feeding type	Xylophagous, phytophagous, mycetophagous, saprophagous, zoophagous,	Freude <i>et al.</i> , 1983; Köhler, 2000	I, II
	Canopy niche	Preferred canopy cover (sunny = 1 to shady = 3)	Möller, 2009; Gossner <i>et al.</i> , 2013; Seibold <i>et al.</i> , 2015	I, III
	Elevation	Preferred elevation zone (planar = 1 to alpine = 5)	Böhme, 2005	I
	Red List status	Categories of for German Red Lists (Ludwig <i>et al.</i> , 2009)	Schmidt <i>et al.</i> , 2016; Schmidl and Büche, 2019	II
Fungi	Body size	Surface of fruiting body (mm ²)	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Decay niche	Preferred decay stage (fresh = 1 to decomposed = 5)	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Wood diameter niche	Preferred dead-wood diameter (small = 1 to large = 4)	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Host tree preference	Broad-leaved, conifer, both, beech specialist	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Fruiting body type	Agaric, polypore	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Range of decay classes	Plasticity of suitable decay stage (1 to 5 stages)	Ryvarden and Gilbertson, 1994; Knudsen and Vesterhold, 2012	I
	Trophic mode	Pathotroph, symbiotroph, saprotroph (wood saprotroph)	Nguyen <i>et al.</i> , 2016	V
	Decay type	Brown rot, white rot, soft rot	Nguyen <i>et al.</i> , 2016	V

In community ecology, species are regarded as entities, and deeper ecological investigations are possible by combining the entities with traits and by defining categories of entities (Petchey and Gaston, 2006). In this thesis, the functional traits of saproxylic beetles and fungi were used to: (i) calculate a trait-based functional diversity of species assemblies (Article I), (ii) calculate community-weighted means of traits (Article III), (iii) separate different trophic modes or feeding types to allow separate analyses (Articles II, V) and (iv) use the Red List status of a species to investigate threatened species separately (Article II).

Traits were compiled from the literature, with the exception of the wing load (body mass divided by wing area) and wing aspect ratio (wing length divided by wing width) of beetles, which serve as proxies for the dispersal ability of beetles (Gibb *et al.*, 2006) and were measured as part of this thesis (Table 1). Traits with respect to the dead wood resource requirements of saproxylic beetles and fungi (i.e., decay niche, wood diameter niche, canopy niche, elevation) were described to determine the mean niche position of a species. To calculate the mean niche position, preference data on an ordinal scale were extracted from the literature (0, not present; 0.5, very rare; 1, rare; 2, common; 3, preferred) and transformed to numeric values following the method described in Gossner *et al.* (2013). The wing load and wing aspect ratio were calculated by measuring the body mass, wing area, wing length and wing width of one sampled specimen per species using an electronic laboratory scale (accuracy of 0.001 mg) and a Leica M205 C microscope (accuracy of 0.001 mm).

3.2.2 Phylogenetic inference

Stochastic and deterministic assembly processes can be discriminated by analyses of phylogenetic turnover (Stegen *et al.*, 2012, 2013). I used this approach to identify the effect of bark coverage on the assembly processes of bacteria and fungi (Article V). For the bacterial phylogeny, the 16S rRNA gene region was directly used for the phylogenetic inferences. The sequences were aligned using MAFFT (Kato and Standley, 2013) and the multiple sequence alignment was then subjected to maximum-likelihood tree inference using FastTree (Price *et al.*, 2009), with parameters as in (Kembel *et al.*, 2014). Fungal phylogeny inferences were performed using the BLASTn best hit for fungal 5.8S rRNA. The sequences were aligned using MAFFT and the topology and branch lengths were estimated using RAxML (Stamatakis, 2014) on the CIPRES Science Gateway (Miller *et al.*, 2011). However, because fungal 5.8S rRNA can be uninformative, averaged taxonomic

distances were also computed (function `taxa2dist`, R package `vegan`, Oksanen *et al.*, 2016) and compared with the patristic phylogenetic distances. The strong correlation between the two matrices in the Procrustes analysis ($R^2=0.90$, $p=0.001$) supported the use of fungal phylogeny inferences for further analyses of assembly processes.

3.3 Statistical analyses

All statistical analyses in this thesis were performed in the free statistical software ‘R’ (www.r-project.org), using additional statistical add-on packages for ‘R’ as needed and as described below.

3.3.1 Functional diversity

The functional diversity of local and regional assemblages of saproxylic beetles and fungi in European beech forest was calculated using a null model approach, to control for variations in the number of species in the different assemblages and to obtain a metric for the assembly patterns (Article I) (Cadotte and Davis, 2016). The used measure of functional diversity describes divergence, i.e. how similar are the species within an assemblage (Cadotte and Davis, 2016). Functional diversity was calculated as the mean pairwise distance (MPD) between functional traits (Table. 1) in the functional space of co-occurring species (Webb *et al.*, 2002; Mouillot *et al.*, 2012). The tip-shuffling method (Cadotte and Davis, 2016) used in the null model provided standardized effects sizes of the MPD (SES MPD), which were calculated with 999 randomizations using the function ‘`ses.mpd`’ in the add-on package `picante` (Kembel *et al.*, 2010). Functional diversity based on species-by-species distance matrices was calculated using the Gower distance (Gower, 1971) of the presence-absence datasets of saproxylic beetles and fungi, using the ‘`gowdis`’ function in the add-on package `FD` (Laliberte and Legendre, 2010). The dissimilarity coefficient of (Gower, 1971) simultaneously combines continuous and categorical traits.

3.3.2 Assembly processes

Ecological processes that influence the assembly of fungi and bacteria within dead wood were explored using a null model approach of phylogenetic turnover to discriminate between stochastic and deterministic assembly processes (Article V; for the fungal and bacterial phylogenies, see Section 3.2.2). Phylogenetic turnover was calculated as the SES of the beta mean nearest taxon distance (β MNTD) (Fine and Kembel, 2011). To retrieve the SES, the β MNTD was first calculated for the original community matrix (observed

β MNTD). Then, the tip labels of the phylogeny were randomized 1000 times and the β MNTD was repeatedly calculated (expected β MNTD). The SES β MNTD was then calculated by subtracting the expected from the observed β MNTD, divided by the standard deviation of the expected β MNTD. Following Stegen *et al.* (2012, 2013), $|\text{SES } \beta\text{MNTD}| > 2$ was interpreted as indicating deterministic turnover and $|\text{SES } \beta\text{MNTD}| < 2$ as indicating stochastic community turnover.

3.3.3 Community composition

Given the enormous variety of different niche requirements of saproxylic species (Stokland *et al.*, 2012), analyses of the turnover in community composition can be more informative than those of species richness in investigations of ecological gradients. Thus, a distance-based analysis of similarity (ANOSIM) was used to test for differences in species community composition among different anthropogenic land-use types (Article II) and between different treatments in the experiments (Articles III, V, VI) (Clarke, 1993). ANOSIM values were calculated for Bray-Curtis dissimilarity distances of presence-absence data using the ‘anosim’ function in the add-on package vegan (Oksanen *et al.*, 2016) and the obtained p-values were adjusted (Benjamini and Hochberg, 1995). As a relative robust method for the visualization of community composition, non-metric multidimensional scaling (NMDS) was used in ordination (Minchin, 1987). Beetles species closely associated with one anthropogenic land-use type were identified using an indicator species analysis (Article II) (De Cáceres and Legendre, 2009).

3.3.4 Linear models

Correlation analyses with linear models were a central part of this thesis research (Articles I–VI). Depending on the data distribution, Depending on the data distribution, linear models were used for Gaussian data (for SESs) and binomial (for browsing of saplings) or quasi-Poisson (for count data of abundance and number of species/molecular taxonomic units) data to account for overdispersion (Dormann, 2017). Due to the nested design (e.g., replicated measurements within the same forest area) of the survey studies and experiments comprising this thesis work, in most cases the linear models were mixed models combining fixed terms and random terms. Simultaneous comparisons of land-use types or treatments with multiple levels were analyzed using multiple comparisons of means by Tukey contrasts, with adjusted p-values for multiple testing, carried out using the function ‘glht’ in the add-on package multcomp (Hothorn *et al.*, 2008). The direct and indirect effects of

the predictors at the regional and local community levels of saproxylic beetles and fungi (Article I) were tested using structural equation modeling, with several linear models analyzed simultaneously (Shipley, 2016). For the analyses of ordinal data on public perception (Article VI), the linear models were replaced with ordinal regression models optimized to handle ordinal data (McCullagh, 1980).

4 Manuscript overview

This thesis includes six articles published in peer-reviewed journals. For each article, the original Abstract, publication status and individual author contributions are provided. The published articles can be accessed in full length via the respective DOI.

In addition, during the time span of this thesis, within a larger framework of forest ecology studies, nine further articles were published, three in peer-reviewed and six in non-peer-reviewed journals. All articles are listed in Appendix B.

Article I

Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests

Jonas Hagge | Nerea Abrego | Claus Bässler | Christophe Bouget | Antoine Brin | Herve Brustel | Morten Christensen | Martin M. Gossner | Jacob Heilmann-Clausen | Jakub Horák | Axel Gruppe | Gunnar Isacson | Frank Köhler | Thibault Lachat | Laurent Larrieu | Jiri Schlaghamersky | Simon Thorn | Livia Zapponi | Jörg Müller

Published 2019 in Journal of Biogeography 46:1054–1065.

<https://doi.org/10.1111/jbi.13556>

Impact factor 2017: 4.154 (29/160 Ecology; 7/49 Geography, Physical)

Aim: Beech forests comprise a globally unique temperate forest type in Europe. The dominance of beech in these forests developed during the ongoing post-glacial northward re-colonization, concurrently with intensified forest use by humans. We investigated how these two processes together with climate shaped the patterns of functional diversity of two major species groups involved in wood decomposition and whether functional diversity is determined on the local or regional species pool level.

Location: European beech forest distribution range.

Taxon: Saproxylic beetles and fungi.

Methods: We analysed records of 532,496 saproxylic beetles of 788 species and 8,630 records of 234 saproxylic fungal species based on sets of traits similar to both groups. We tested how space, climate and landscape composition affect trait-based functional diversity on local and regional scales. Using structural equation modelling, we tested whether functional diversity is shaped on the local or regional scale.

Results: The response of local functional diversity of both saproxylic beetles and fungi followed a highly congruent pattern of decreasing functional diversity towards the north, with higher elevation and accounted for overall geographical gradients with higher temperature, while increasing with higher precipitation. Structural equation modelling revealed that local functional diversity is determined by community changes operating on the level of the regional species pool.

Main conclusions: Our findings suggest that the functional diversity patterns of saproxylic organisms in European beech forests are mainly determined on the regional scale and driven by anthropogenic and biogeographical processes. To conserve the variation and hotspots of functional diversity in beech forests, activities have to focus on a broad spatial and climatic range of sites throughout Europe, including the primeval forests in the east, as started by the UNESCO World Heritage selection of “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe”.

Individual contributions: For this macroecological study I compiled a dataset on beetles and fungi across European beech forest, which originate from several local and country-level species surveys. I ordered and homogenized the data from the different sources, checked for different taxonomy and controlled outliers. Trait data for beetles and fungi I gathered from published trait data or extracted them from primary literature. Environmental data for sample sites I extracted from free spatial databases (*data acquisition: 80%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 100%*). I wrote and revised the manuscript for the article (*writing and revising: 90%*). The basic idea and concept of the manuscript was developed together with the coauthors of the article and I further developed the idea of the article and derived the specific hypotheses (*concept: 60%*).

Beetle biodiversity in anthropogenic landscapes with a focus on spruce plantations, Christmas tree plantations and maize fields

Jonas Hagge | Sebastian Seibold | Axel Gruppe

Published 2019 in Journal of Insect Conservation 23:565–572.

<https://doi.org/10.1007/s10841-019-00146-w>

Impact factor 2017: 1.562 (33/96 Entomology)

In Europe, anthropogenic habitats that are optimised for agriculture and forestry purposes have widely replaced natural habitats. To assess their value for biodiversity, we compared beetle communities among three anthropogenic land use types, namely spruce plantations, Christmas tree plantations and maize fields. These three land use types are all characterised by high phytobiomass and vertical plant structure and represent a gradient of anthropogenic impact linked to fertilisation, pesticide use, frequent operation of machinery and rotation period length. We found that all components of beetle diversity, i.e. abundance, number of species and Simpson diversity as well as the number of threatened beetle species decreased with increasing anthropogenic impact from spruce plantations to Christmas tree plantations to maize fields. However, beetle biomass was relatively high in maize fields, due to the abundant species in this land use type having a high body mass. Community composition changed with anthropogenic impact. Beetle communities in maize fields were characterised by a higher frequency of zoophagous beetles and a lower frequency of saprophagous/mycetophagous and xylophagous beetles than those in Christmas tree plantations and spruce plantations. The low value of maize fields for beetle biodiversity is concerning because the area covered by maize increased over the last decade by 26.7% and now constitutes 13.5% of arable land globally.

Individual contributions: I received the raw field data and the data of the determined beetle species. I ordered and handled the data and merged it with species trait data and Red list information (*data acquisition: 15%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 100%*). I wrote and revised the manuscript for the article (*writing and revising: 90%*). I used the established sampling design and species survey to develop the concept of the manuscript and the particular research questions (*concept: 60%*).

Article III

Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation

Sebastian Seibold* | Jonas Hagge* | Jörg Müller | Axel Gruppe | Roland Brandl | Claus Bässler | Simon Thorn

* Both authors contributed equally.

Published 2018 in Forest Ecology and Management 409:564–570.

<https://doi.org/10.1016/j.foreco.2017.11.052>

Impact factor 2017: 3.169 (4/66 Forestry)

Vertical gradients of habitats are a typical characteristic of forest ecosystems. Sun-exposed dead wood in the upper canopy, for instance, provides a habitat for saproxylic beetles distinct from that in the more shaded dead wood below the canopy. Canopy research, however, is challenging due to both the limited accessibility and potential confounding effects of temperature on trapping probability when activity traps are used. We studied saproxylic beetle assemblages along a complete vertical gradient without bias caused by temperature effects on activity. Using crane-like constructions attached to the top of large Silver Fir trees (*Abies alba*), we exposed bundles of freshly cut branches of European Beech (*Fagus sylvatica*), Silver Fir and Norway Spruce (*Picea abies*) in three different vertical strata (upper canopy, mid-canopy and near the ground). The bundles in the upper canopy were fully exposed to the sun and the bundles in the mid-canopy and near the ground were in the shade. We allowed beetles to colonize the bundles of branches for one growing period and then reared beetles from each bundle over three years. The species composition of saproxylic beetle assemblages differed between bundles in the upper canopy and near the ground; bundles in the mid-canopy had an intermediate assemblage composition. The abundance of saproxylic beetles was higher near the ground than in the upper canopy, whereas the number of species showed the opposite pattern. Overlapping confidence intervals of sample-based rarefaction and extrapolation curves for species diversity indicate that estimated gamma diversity per stratum is similar across the three strata. Our results support earlier studies that revealed the importance of habitat heterogeneity as a driver of the biodiversity of taxa associated with dead wood. As we controlled for wood diameter and tree species diversity, our study suggests that the

microclimatic variability within dead wood – and thus habitat heterogeneity for saproxylic beetles – is higher in the upper canopy than near the ground. For biodiversity conservation in forests, our results support a strategy of enhancing the number of trees with microhabitats, particularly those with dead branches in the upper tree crown. Dead branches and standing dead trees should only be removed, e.g. for safety reasons, if no other option is available.

Individual contributions: The field experiment for this article took three years and I took over the field work for the third year: collecting the insects and sorting the samples. I organized the species identification and gathered the species dataset for all the three years. I conducted the morphological trait measurements (i.e., wing load and wing aspect ratio) for the sampled beetle species (*data acquisition: 40%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 100%*). I wrote the Method and Result section alone and drafted the first version of the Introduction and Discussion (*writing and revising: 50%*). The basic idea and concept of the manuscript was developed together with the coauthors, in particular the second shared first author of the article (*concept: 20%*).

Deadwood retention lowers the browsing pressure of overabundant deer

Jonas Hagge | Jörg Müller | Claus Bässler | Samantha Susanne Biebl | Roland Brandl | Matthias Drexler | Axel Gruppe | Stefan Hotes | Torsten Hothorn | Peter Langhammer | Hans Stark | Roland Wirtz | Veronika Zimmerer | Atle Mysterud

Published 2019 in Forest Ecology and Management 451:117531.

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Impact factor 2017: 3.169 (4/66 Forestry)

Humans have widely extirpated large carnivores and simultaneously promoted overabundances of deer. The intense pressure imposed by these herbivores in forests has led to extremely low rates of natural forest regeneration. In natural old-growth forests, deadwood functions as a key driver of biodiversity and promotes ecosystem functioning, such as water retention and nutrient recycling. An as yet unappreciated function of deadwood is its ability to act as a physical barrier, excluding large herbivores from a given patch and thereby reducing browsing pressure. However, this benefit may be minimized by an increase in rodent herbivory in the sheltered patches. In this study, a field experiment was conducted in a total of 384 plots in which tree crowns (0–4) from logging residuals were used as increasingly dense physical barriers to shelter five newly planted saplings of silver fir (*Abies alba* Mill.). Generalized linear mixed-effects models were applied to determine whether sapling browsing by roe deer and rodents was differentially affected by these barriers. The probability of roe deer browsing decreased from 26% (no crowns) to 2% (4 crowns) while that of rodent browsing increased from 1% to 17%, respectively, as the number of deadwood crowns used in barrier construction increased. In broadleaf stands, browsing by roe deer and rodents was generally higher than in coniferous stands. In forests with high numbers of visitors, browsing by roe deer was reduced, but browsing by rodents was not influenced. The retention of large amounts of deadwood or active deadwood increments may thus provide an effective barrier to roe deer browsing but promote the browsing activity of rodents. The landscape-level heterogeneity of browsing patterns associated with the presence of deadwood suggests that deadwood shelters in homogenized

forests may encourage both natural forest regeneration and forest biodiversity, despite an overabundance of roe deer.

Individual contributions: I devolved the sampling protocol and carried out data collection in the entire study area of southern Germany with support of one bachelor and one master student. I gathered and handed the final dataset for the analyses (*data acquisition: 75%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 90%*). I wrote and revised the manuscript for the article (*writing and revising: 80%*). The basic idea and concept of the manuscript was developed together with the coauthors of the article (*concept: 60%*).

Bark coverage shifts assembly processes of microbial decomposer communities in dead wood

Jonas Hagge | Claus Bässler | Axel Gruppe | Björn Hoppe | Harald Kellner | Franz-Sebastian Krahl | Jörg Müller | Sebastian Seibold | Elisa Stengel | Simon Thorn

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Impact factor 2017: 4.847 (9/85 Biology; 18/160 Ecology; 8/49 Evolutionary Biology)

Bark protects living trees against environmental influences but may promote wood decomposition by fungi and bacteria after tree death. However, the mechanisms on how bark determines the assembly process and biodiversity of decomposers remain unknown. Therefore, we partially or completely removed bark from experimentally felled trees and tested with null modelling whether assembly processes were determined by bark coverage and if biodiversity of molecular sampled fungi and bacterial generally benefited from increasing bark cover. The community composition of fungi, wood-decaying fungi (subset of all fungi), and bacteria clearly separated between completely debarked, partly debarked and control trees. Bacterial species richness was higher on control trees than on either partly or completely debarked trees whereas the species richness of all fungi did not differ. However, the species richness of wood-decaying fungi was higher on partially and completely debarked trees than on control trees. Deterministic assembly processes were most important in completely debarked trees, a pattern consistent for fungi and bacteria. This shift might have been a general reaction of species assemblies to conditions that alter habitat characteristics such that they are no longer the natural, dominant ones.

Individual contributions: I received the molecular data for this manuscript. I further processed the data and collected taxonomic information and species traits for the sequence data. I repeated the field sampling for this experiment in 2018, however these data are still to processes and not part of the current manuscript (*data acquisition: 15%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 100%*). I wrote and revised the manuscript for the article (*writing and revising: 90%*). The basic idea and concept of the manuscript was developed together with the coauthors of the article (*concept: 50%*).

Reconciling pest control, nature conservation, and recreation in coniferous forests

Jonas Hagge | Franz Leibl | Jörg Müller | Martin Plechinger | João Gonçalo Soutinho | Simon Thorn

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Impact factor 2017: 7.279 (2/57 Biodiversity Conservation)

Protected areas are not only crucial for biodiversity and natural processes but also for recreation. Although a benign neglect strategy of dealing with natural disturbances in protected areas is beneficial for nature, public debate on avoiding increased pest population growth has intensified. We evaluated the effect of mechanical pest control measures in decreasing populations of insect pests, maintaining nontarget biodiversity, retaining high recreational value, and keeping economic costs low. Debarking and bark scratching or gouging effectively prevented infestation of felled trees by European spruce bark beetles (*Ips typographus*) and controlled the beetles in recently infested trees. Bark scratching or gouging retained biodiversity at natural levels, whereas debarking decreased biodiversity by 54% with higher economic costs. The public rated bark-gouged trees more positively than debarked trees. We thus urge authorities to promote bark scratching or gouging in the control of bark beetles in protected areas instead of salvage logging and debarking.

Individual contributions: I established the experiment for this article, conducted the field work, sort the insect samples and organized the dataset (*data acquisition: 90%*). I conducted the data analysis independently and designed and produced the figures (*data analysis and figures: 100%*). I wrote and revised the manuscript for the article (*writing and revising: 90%*). The basic idea and concept of the manuscript was developed together with the coauthors of the article (*concept: 60%*).

5 Discussion

The main objectives of this thesis were to investigate the relationships between saproxylic organisms and their environment and then determine the impact of human activities on these relationships. The obtained ecological information was then synthesized from a conservation-oriented-management perspective.

This thesis showed that in European beech forests, the relationship between saproxylic organisms and their environment is simultaneously affected by biogeographical history, climate and human land-use. The functional diversity of saproxylic beetles and fungi decreases along a historical re-colonization gradient of European biota from south to north. A climate regime suitable for European beech has promoted the functional diversity of associated saproxylic taxa. However, urban areas of increasing size and increased land-use intensity has decreased the functional diversity of saproxylic beetles and fungi along an east-west continental gradient. Although saproxylic beetles and fungi completely differ in their biology and in their functions in wood decomposition, the functional diversity patterns of the two groups in European beech forests are highly congruent. For both, functional filters operate on a regional scale in different forests, with the local scale simply being a blueprint thereof (Article I). Anthropogenic habitats poorly support beetle conservation while an increased anthropogenic impact on the landscape further lowers biodiversity (Article II). A distinct feature of forest ecosystems is their pronounced vertical axis, which has favored the emergence of different assembles of saproxylic beetles at different vertical strata. For the same amount and type of dead wood, a larger number of species is supported in the uppermost canopy than near-ground. Dead branches in the canopy should thus be retained as much as possible to support the diversity of saproxylic species (Article III). Dead wood as a structural feature on the forest floor acts as a refugia, protecting saplings from browsing by roe deer, and thus may ultimately promote natural regeneration processes. However, compensatory browsing by smaller-herbivore guilds (i.e., rodents) in the shelter of dead wood may lower this effect in regions or years of high rodent density (Article IV). Bark cover was found to be among the factors that control assembly processes in the colonization of dead wood. For saproxylic fungi and bacteria, deterministic assembly processes were more relevant on trees without bark; however, the effects of bark on biodiversity patterns differed between bacteria and fungi and between the processes of fungal colonization and fructification. This complexity obscures the overall positive effect of bark cover on the biodiversity of saproxylic microorganisms

(Article V). An evaluation of mechanical bark manipulation for pest control of the European spruce bark beetles (*I. typographus*) revealed that bark gouging (i.e. removing bark only in strips) is effective in preventing infestations of weakened trees and in controlling *I. typographus* in recently infested trees. Moreover, bark gouging retains biodiversity at natural levels, whereas the originally recommended strategy of debarking decreases biodiversity by 54% and incurs higher economic costs. The public rated bark-gouged trees more positively than debarked trees. The potential to combine factors relevant to the management of protected areas (Figure 4a) supports the use of bark gouging, rather than salvage logging and debarking, in the control of bark beetles in protected areas (Article VI).

5.1 Appropriate sampling methods for saproxylic species

In biodiversity studies, the appropriate sampling method depends on the research objective and the target species group and must be carefully chosen. For the sampling of saproxylic insects, there is wide variety of active and passive sampling methods (Köhler, 2000). Field surveys of fruit bodies are used for saproxylic fungi, although new methods allowing the passive collection of fungal spores were recently described (Abrego *et al.*, 2018). For saproxylic fungi, insects and bacteria, a powerful approach consists of integrative environmental samples in which species are identified by DNA barcoding based on next-generation sequencing technologies (Stokland *et al.*, 2012; Morinière *et al.*, 2016; Purahong *et al.*, 2018).

In this thesis, the sampling methods used to investigate saproxylic biodiversity depended on the species group and the specific objectives. Beetles, as a mobile taxon, were sampled with passive continuously collecting traps (i.e., flight-interception traps and Malaise traps), which have the advantage of integrative habitat sampling. A closer focus on dead wood as a resource and habitat of saproxylic beetles was obtained by object-oriented sampling with emergence traps (i.e., closed trap covering the surface of dead wood in the field such that every insect emerging from the dead wood is trapped) and by the rearing of baited dead wood objects (i.e., placing dead wood from the field in closed containers and sampling all emerging insects). A potential disadvantage of emergence traps attached to dead wood objects in the field is that they might not be completely closed, because of irregularities and desiccation cracks in the bark. Consequently, some species may be lost (given the morphological adaptations of saproxylic species to live under the bark or in small cracks in the wood) while others may enter the emergence trap from the

outside (see the Discussion in Thorn, Bässler, Bußler, *et al.*, 2016). Rearing dead wood in fully closed containers avoids this problem but the environmental conditions will be different from those in the field, tending to be moister and vulnerable to overheating. These critical points can be partly prevented by placing rearing containers under a roof at ambient temperature, to provide shade and avoid overheating, and by allowing air circulation via fine mesh covers of openings made on both sides of the containers (Article III). Sampling the same dead wood log simultaneously with an emergence trap and rearing, as done in this thesis, yield highly correlated measures of saproxylic biodiversity (Article IV). This result is valuable for further research requiring the object-oriented sampling of saproxylic insects. A further crucial point is that, even for dead wood of small dimensions (i.e., branches), rearing should be conducted for several years, as in our study some species, such as *Hylobius abietis* (L., 1758) and *Cryphalus piceae* (Ratzeburg, 1837) (phloem feeders), were recorded only in the first and second year, and those with typical larval development times of > 1 year, such as *Clytus lama* Mulsant, 1847 and *Clytus arietis* (L., 1758), only after 3 years of continuous rearing (Article III). In general, emergence traps and rearing yield fewer insect individuals than flight-interception traps and Malaise traps. These differences may hamper statistical analyses (Birkemoe and Sverdrup-Thygeson, 2015; Plewa *et al.*, 2017). Therefore, sampling by both emergence traps and rearing should cover a sufficient amount of the sampled resource.

Fungal fruit-body inventories provide only a glimpse of the fungal community, as only a minority of fungal species in dead wood form fruit bodies and fructification can be unpredictable and short-term (Ovaskainen *et al.*, 2013). Nevertheless, fruit-body and molecular inventories often yield comparable fungal diversity patterns, and the most abundant species identified by molecular surveys commonly correspond to those identified by fruit-body inventories (Ovaskainen *et al.*, 2013; Frøslev *et al.*, 2019). In the analyses of the effect of bark coverage on microbial biodiversity, performed as part of this thesis, there was no evidence that bark coverage (i.e., control, partly debarked, completely debarked) significantly influenced the species number (i.e., number of operational taxonomic units, OTUs) of fungi, as determined by molecular means. For the subset of wood-decaying fungi species, molecular analyses even revealed lower numbers on control trees than on partly and completely debarked trees (Article V). These molecular determinations of the species richness of fungi contradict previous fruit-body inventories of the same felled trees, which showed a lower fungal species richness on debarked trees (Thorn, Bässler, Bußler, *et al.*, 2016). Thus, bark coverage shapes both processes: firstly, the colonization of dead trees,

which determines the community of wood-inhabiting fungi sampled by molecular means, and secondly, the number of species able to produce fruit bodies and thus be detected in a fruit-body inventory. These findings demonstrate the importance of the sampling method used in studies of wood-inhabiting fungi and the need to tailor the sampling method to the research objective. A deeper understanding of assembly processes will require the use of both fruit-body and molecular inventories (Frøslev *et al.*, 2019).

5.2 Drivers of saproxylic biodiversity in European beech forest

European beech forests dominate temperate forests in Central Europe (Peters, 1997). Among Central European saproxylic beetle species, ~70% may reside in beech-dominated forests, highlighting the important function of these forests in saproxylic conservation (Müller *et al.*, 2012). The work performed for this thesis contributes to a deeper understanding of how the trait-based functional diversity of saproxylic beetles and fungi in European beech forests is affected by the environment and by human activity. Functional diversity is a measure of biodiversity as it relates to ecosystem functioning (Hooper *et al.*, 2005). In terms of changes in the ecosystem, the effect of functional diversity is more pronounced than that of species richness and its analysis can thus provide a deeper understanding of the drivers of biodiversity (Flynn *et al.*, 2009). Article I showed that the functional diversity of European beech forests is mainly determined on a regional scale and is simultaneously driven by biogeographical and anthropogenic processes.

For saproxylic beetles and fungi, functional diversity in European beech forests decreases along a historical re-colonization gradient from south to north, in a pattern reflecting the biogeographical history of the Quaternary climatic oscillations of glacial and inter-glacial periods (Ehlers and Gibbard, 2004). During cold periods, species migrate to refugia mainly in Mediterranean regions and during warm periods re-colonize previous habitats to the north (Hewitt, 2000). Saproxylic organisms are obligatorily linked to dead wood both as resource and habitat. Thus, in European beech forests saproxylic beetles and fungi are also linked to the biogeographical history of these trees. The phylogeographical pattern of *F. sylvatica* also well reflects the Quaternary climatic oscillations in Europe (Magri *et al.*, 2006; Magri, 2008) and, as demonstrated in this thesis, thereby also impacts associated saproxylic organisms. For the saproxylic beetle species *Rosalia longicorn* (*Rosalia alpina* L., 1758), its phylogeography was shown to closely parallel that of European beech, its main host, reflecting their common history (Drag *et al.*, 2018). A further example is the close link between the species richness of understory plants in

European beech forests and the biogeographical history of those forests (Willner *et al.*, 2009). The functional traits of saproxylic beetles and fungi were found to be more clustered in the north than in the south, indicative of a shift in the dominant assembly pattern of saproxylic organism from a more random ecological drift in the south to habitat filtering in the north. In other words, community composition and structure in the northern range of European beech forests might not yet have reached equilibrium with the environment. This finding is consistent with the ongoing re-colonization of European beech towards the north in Sweden and towards the northeast in Poland (Latalowa, 1992; Björkman, 1996; Magri, 2008). Whether the latitudinal gradient should be considered in macroecological studies as a gradient of biogeographical history or as a climatic gradient of declining temperature remains a subject of critical discussion, and how to disentangle these two gradients is unclear (Lomolino *et al.*, 2016). However, this is not the case in European beech forests, where the temperature decline in the north is counteracted by an elevation decline that covers the distribution range of the forests (Article I). This strengthens the underlying effect of biogeographical history on the functional diversity of saproxylic beetles and fungi in European beech forests.

Land-use intensity was shown to have a negative effect on the functional diversity of saproxylic beetles and fungi in European beech forests on the landscape scale (i.e., the proportion of urban area within a 3-km radius). Higher land-use intensity thus strengthens the effect of habitat filtering on species assemblages, resulting in a lower functional diversity and ultimately in functional homogenization, as reported for taxonomic diversity (Gossner, Lewinsohn, *et al.*, 2016). The functional diversity decrement described in Article I suggests that species loss is not a random process; rather, because of particular functional traits, some species are more strongly affected than others. This was shown in a model of the extinction risk of saproxylic beetles (Seibold *et al.*, 2015). On the continental scale, the communities of saproxylic beetles are functionally more diverse in eastern than in western Europe, which follows human land-use history on the continent (Rose, 1992; Peterken, 1996) and the older age of beech forests in the east (e.g., in the Carpathians).

The functional diversity of saproxylic beetles and fungi was filtered mainly on the regional scale of different forests, with local functional diversity following the regional pattern. This finding well agrees with the beta-diversity patterns of saproxylic beetles in European beech forests, where species turnover is highest, as determined based on comparisons of different forest areas (Müller *et al.*, 2012). Jiménez- Alfaro *et al.* (2018) also showed that biogeographical and climatic factors filter plant species richness in

European beech forests on the regional species pool level and that small operative habitat conditions only serve to further alter local species diversity. Thus, to conserve hotspots of functional diversity in beech forests, forest management activities must be aimed at a broad spatial and climatic range of sites throughout Europe. Conservationists and politicians have to reinforce their efforts to promote and expand suitable European-wide conservation strategies, such as the Natura 2000 network, consisting of 13 different European beech forest habitat types, including four priority habitat types and the UNESCO World Heritage of “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe.” The congruent results regarding the functional diversity of saproxylic beetles and fungi, as reported in this thesis, provide an opportunity to protect areas with a high functional diversity for both hyper-diverse wood decomposing taxa.

5.3 Potential of forestry and agriculture production sites for beetle biodiversity

Comparisons of the beetle conservation potential of spruce plantations, Christmas tree plantations and maize fields revealed a generally low potential for all three habitats. All measures of beetle diversity decreased with increasing anthropogenic impact, from spruce plantations to Christmas tree plantations to maize fields. This decline in biodiversity as a function of anthropogenic land-use type can be explained by the high levels of fertilizer and pesticide use, the frequent operation of machinery and the short duration of the crop rotation period, all of which have been implicated in the loss of biodiversity (Kleijn *et al.*, 2009; Newbold *et al.*, 2015; Gossner, Lewinsohn, *et al.*, 2016). Despite the high phytobiomass and a vertical plant structure of the investigated anthropogenic habitats, their potential as surrogate habitats for threatened species is low. Only 0.5% of the beetles sampled from those habitats belonged to species of conservation concern with a decreasing number with increasing anthropogenic impact from spruce plantations to Christmas tree plantations to maize fields. Besides the obvious negative effects of pesticide use, anthropogenic habitats lack the structures (e.g., dead wood) and structural heterogeneity of natural habitats as well as spatial and temporal habitat continuity, which are important factors especially for threatened species (e.g. Kolb and Diekmann, 2004; Stokland *et al.*, 2012; Eckelt *et al.*, 2018). Maize fields were characterized by a few dominant species with high abundances, whereas the species frequency was more balanced in Christmas tree and spruce plantations. This suggests species homogenization at the landscape level, by the loss of threatened and specialist species. Biotic homogenization rather than local diversity loss may be the most substantial consequence of land-use intensification (Gossner, Lewinsohn,

et al., 2016). In the current discussion of insect decline, a topic of interest is beetle biomass, because it is linked to productivity (Hallmann *et al.*, 2017). Maize fields have a relatively high beetle biomass, due to the high body mass of the abundant species present in this land-use type. Thus, a few abundant beetle species able to cope with the high land-use intensity characteristic of maize fields [e.g. *Harmonia axyridis* (Pallas, 1771), *Cantharis lateralis* L., 1758, *Hemicrepidius hirtus* (Herbst, 1784)] may be able to make use of the high and rapidly developing amounts of phytobiomass. In general, the results reported herein, based on investigations of three abundant anthropogenic land-use types in Central Europe, provide a case study of beetle biodiversity and support previous studies showing that land-use intensification is a major driver of biodiversity loss (Sala *et al.*, 2009; Allan *et al.*, 2014). The very low potential for beetle diversity and the relatively low number of beetle species of conservation concern in maize fields is alarming because 13.5% of arable land globally is covered by maize fields, a value that represents a 26.7% increase over the last decade (FAO, 2018).

5.4 Functioning of dead wood from the forest floor to the canopy

The studies comprising this thesis provide further evidence that dead wood is a keystone structure in forests, one that is essential for saproxylic biodiversity and serves as a structural element in multiple processes in forests ecosystems (Stokland *et al.*, 2012). In the browsing experiment described in Article IV, a physical barrier consisting of dead wood crowns on the forest floor decreased the probability of roe deer browsing of fir saplings in Central European commercial forest from 26% to 2%. Roe deer have become overabundant in this area due to unbalanced forest management strategies (Putman, 1992; Côté *et al.*, 2004). This result revealed the opportunity to shelter saplings from browsing and may thus ultimately promote natural forest regeneration. Economic losses due to roe deer browsing are high and in Germany millions of Euro are spent annually on conventional methods of browsing protection (e.g., fencing) (Clasen and Knoke, 2013). The retention of tree crowns from logging residuals at the place of origin offers a low-cost method of protecting saplings from roe deer browsing and may ultimately promote natural forest regeneration. In addition, the coincident accumulation of dead wood in the forest supports saproxylic biodiversity and ecosystem functioning. In addition to the increased structural diversity on the forest floor, dead wood functions as a temperature and moisture buffer and prevents the runoff of forest litter and other sources of nutrition (Stokland *et al.*, 2012). Thus, dead wood on the forest floor also supports the biodiversity of non-saproxylic arthropods (Seibold,

Bässler, Baldrian, *et al.*, 2016). In addition, it offers shelter from predators, nesting sites, an enhanced food supply and a suitable humid microclimate for rodents (Carey and Johnson, 1995; Suter and Schielly, 1998). This was evident in the browsing experiment, in which the physical barrier formed by dead wood increased the browsing probability of rodents, from 1% on the plots with no dead wood crowns to 17% on plots with four dead wood crowns. In fact, rodent browsing facilitated by dead wood may compensate or even negate the positive effect of dead wood in reducing roe deer browsing in regions and years of high rodent density.

Not only the horizontal distribution of dead wood on the forest floor but also the vertical distribution from the forest floor to the canopy is a distinct feature of forests (Nakamura *et al.*, 2017). The vertical dead wood experiment described in Article III showed differences in the composition and alpha diversity of saproxylic beetle assemblages in dead branches placed at different vertical strata. The community composition gradually changed from the forest floor to the upper canopy, with distinct communities between near-ground and the upper canopy. The clear differences are in line with several other studies on saproxylic beetles in the canopy (Ulyshen and Hanula, 2007; Vodka *et al.*, 2009; Foit, 2010; Maguire *et al.*, 2014; Weiss *et al.*, 2016; Plewa *et al.*, 2017). Saproxylic beetles were most abundant near-ground, but the number of species was highest in the upper canopy. Gamma diversity, however, did not differ between strata. Because the size, amount and tree species composition of the exposed dead wood bundles used in the experiment were standardized, the observed niche differentiation for saproxylic beetles along the vertical axis must have been the product of interacting environmental factors. The most obvious was the penetration rate of solar radiation, as < 5% of solar radiation reaches the forest floor of a dense temperate forest (Hutchinson and Matt, 1977). Given that insects operate on small scales, the structural features of the vegetation and the consequences for the microclimate are highly relevant for diversity and assembly processes (Müller, Bußler, and Kneib, 2008; Hilmers *et al.*, 2018). For dead wood on the forest floor, the impact of available solar radiation on saproxylic beetles is well documented (Seibold, Bässler, Brandl, *et al.*, 2016). Thus, the community turnover determined in the experiment would mainly have been driven by dead wood niche differentiation as result of solar radiation, with warmer and drier dead wood in the canopy. However, to distinguish between the roles of vertical position and sun exposure requires further experiments comparing beetle assemblages along vertical and horizontal gradients of sun exposure (see Section 5.7). The amount of community turnover and the higher number of species in the canopy indicate that dead

wood in the canopy increases the diversity of dead wood in the forest and thus is of considerable importance in the conservation of saproxylic beetle biodiversity. Activities that reduce amounts of these types of dead wood, such as cutting dead branches or dead trees for safety reasons or harvesting logging residuals as fuel, may threaten the biodiversity of saproxylic beetles. Dead wood in the upper canopy develops only slowly, as a result of tree senescence, and should be preserved as much as possible, such as by retaining trees bearing a large number of dead branches in their canopies as habitat trees. The cutting of dead branches or the felling of dead trees should be the very last option when safety measures must be considered and appropriate actions taken (see Stokland *et al.*, 2012 p. 399 for a decision tree). Other options, such as restricting access to the trees or informing visitors of the importance of dead branches, should be given priority.

5.5 Bark beetle management and bark as an important control variable

In Europe, > 39% of the protected areas are in coniferous forests naturally susceptible to bark beetle outbreaks (Article VI). Pest management is one of the main justifications for interventions in protected areas, despite the harm done to conservation (Müller *et al.*, 2018). A prominent example is the Bavarian Forest National Park, where ~18% of bark beetle infested areas (1200 ha) have been salvage logged, in compliance with mandatory pest management (Mehr *et al.*, 2012). The results presented herein suggest an alternative approach to pest control, one that is optimized for the simultaneous protection of biodiversity and major reductions in bark beetles. Bark gouging, i.e., the removal of strips of bark using a newly developed mechanical bark gouging device (Figure 4c), was shown to be an efficient method of preventive pest control (i.e., before the colonization of felled trees by *I. typographus*) and as effective as debarking. Moreover, bark gouging 2 and 5 weeks after colonization decreased the abundance of *I. typographus* by 80–90%, which did not significantly differ from preventive bark gouging. Thus, bark gouging on-site for recently infested trees is as effective as the removal of infested trees by salvage logging, which decreases the abundance of *I. typographus* to ~10% of an untreated control (Thorn *et al.*, 2014), and can be applied both preventively and on trees recently infested by *I. typographus*.

Unlike salvage logging, bark gouging and debarking allow disturbance affected trees to remain in the forest and dead wood to accumulate by natural processes, resulting in amounts 10–20 times higher than in salvage logged areas (Müller *et al.*, 2010). However, whereas complete removal of the bark layer of dead trees by debarking decreases

saproxylic beetle biodiversity by 54%, bark gouging, whether applied preventively or on recently infested trees, retains biodiversity at natural levels. Moreover, gouging logs is 28% cheaper than debarking. If the bark-gouging device had been developed 12 years ago and consistently used thereafter in the Bavarian Forest National Park, 1.6 million Euros would have been saved so far. Furthermore, although logs with undamaged bark were the most positively perceived by the general public, bark-gouged logs ranked second, while debarked logs evoked a negative reaction. This finding extends earlier findings at the landscape scale, in which green trees were more positively perceived than trees affected by disturbances at the scale of a single trunk (O'Brien, 2006; Clement and Cheng, 2011; Hartel *et al.*, 2017). The negative perception of completely debarked logs can therefore be explained by their relatively non-natural appearance, which would favor a non-intervention strategy in forests. Nonetheless, if pest control is required, bark gouging will be more positively perceived than debarking. These combined advantages of bark gouging, i.e., effective pest control, the protection of biodiversity, cost-efficient management and a favorable public perception, recommend its use over debarking or salvage logging in protected areas. The advantages become even more relevant when considered against a background of natural disturbances and an increased frequency and severity of bark beetle eruptions (Seidl *et al.*, 2011, 2014, 2017). Furthermore, these results underline the importance of considering multiple aspects to achieve effective evidence-based management of disturbed forests stands.

A second experiment performed for this thesis (Article V) that also relied on manipulating bark coverage (i.e., bark removal experiment) demonstrated the general relevancy of bark as a controlling variable for the assembly of saproxylic organisms. Molecular analyses of sampled fungi, wood-decaying fungi (subset of all fungi) and bacteria showed that bark coverage of experimentally felled Norway spruce trees explained ~15% of community dissimilarity, with a gradual shift of the communities from control to partly debarked to completely debarked trees. Communities of fungi, the subset of wood-decaying fungi, and bacteria in completely debarked trees were shaped by higher amount of deterministic processes. Thus, natural events and anthropogenic activities (i.e., pest management, logging) that result in bark removal from dying trees change the assembly processes of microbial communities such that deterministic processes become more relevant. This finding is supported by other studies showing that anthropogenic disturbances and additional factors that shift habitats away from their predominant status increase the importance of deterministic processes in community assembly (Chase, 2007;

Smith *et al.*, 2009; Püttker *et al.*, 2014). In other words, if a habitat is changed such that evolutionarily established niches and biotic interactions are changed as well, then deterministic processes will increase in relevance.

Bacterial species richness was found to be higher on logs with bark than on partly or completely debarked logs. This positive effect can be explained by the ability of bark to buffer moisture (Cornwell *et al.*, 2009) and by the increased niche range provided by the energy-rich and structurally complex bark layer (Dossa *et al.*, 2016). Both lead to an increased biodiversity of bacteria (Clausen, 1996). By contrast, the species richness of fungi did not respond similarly, and a higher number of wood-decaying fungal species was even found on partly and completely debarked trees than on control trees. This finding suggests that bark removal promotes the co-occurrence of wood-decaying fungal species by relaxing the competitive pressure exerted by strongly competitive wood-rotting species (Maynard *et al.*, 2017). This concept is also supported by the competitive wood-rotting red-belted bracket (*Fomitopsis pinicola* (Sw.) P. Karst.) (Vogel *et al.*, 2017), which in this thesis was found to dominate the community on trees with intact bark but had a comparable lower rank position in debarked trees. In experimentally manipulated fungal communities, increasing the number of co-occurring species reduced wood decomposition by 30% (Fukami *et al.*, 2010). Thus, this thesis gave further support, that function and species diversity are not always positively correlated (Fukami *et al.*, 2010; Maynard *et al.*, 2017) and that bark is among the factors controlling assembly processes and biodiversity in dead wood.

5.6 Recommendation for forest nature conservation

A main objective of this thesis was to contribute to evidence-based nature conservation strategies in forests. In each of the six articles of this thesis, management options based on the results were proposed and potential gaps in current conservation strategies identified, focusing on saproxylic biodiversity. Some of these recommendations are applicable at the continental scale and others to local dead wood management. Accordingly, they are addressed to political decision-makers, government authorities, conservationists and local foresters. The six recommendations from the respective articles can be summarized as follows:

Recommendation 1: To protect the range of saproxylic functional diversity in European beech forests and thus ecosystem functioning, there is a need for a

comprehensive network of protected areas representing the geographical and climate range of European beech forests, such as the UNESCO World Heritage selection of “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe.” Additional sites for protection must encompass a broad spatial scale to include the different regional beech forest types, including the primeval forests in Eastern Europe.

Recommendation 2: Anthropogenic habitats optimized for wood production or agriculture do not support beetle conservation and their spread will further lower biodiversity. The management of anthropogenic habitats should instead follow an integrated approach that includes the retention of natural structures and natural disturbances through ecologically sustainable management.

Recommendation 3: Dead branches in the canopy offer a habitat unlike that of near-ground dead wood and support a distinct, species-rich saproxylic beetle community. Thus, dead wood in the upper canopy should be retained as much as possible, such as by retaining trees with a large number of dead branches in the canopy as habitat trees. The cutting of dead branches or felling of dead trees should be the very last option when safety measures must be taken.

Recommendation 4: Dead wood crowns from logging activities should be retained in the forest, because it simultaneously provides an efficient physical shelter that protects saplings from roe deer browsing and promotes saproxylic biodiversity. However, in years and regions with high rodent density, the positive effect of dead wood on browsing reduction can be abrogated by higher rodent browsing in shelter of dead wood crowns.

Recommendation 5: Management activities effecting the natural creation of dead wood or that actively create dead wood as a restoration measure should mimic natural processes to avoid interfering with natural assembly processes and ecosystem functioning.

Recommendation 6: If pest control of the European spruce bark beetle (*I. typographus*) is required in protected areas, bark gouging is recommended as the on-site method of bark beetle reduction rather than salvage logging or debarking. The advantage of bark gouging is that it simultaneously achieves biodiversity protection, economic savings and a positive public perception.

5.7 Future directions

Conservation goals should be the product of the best available knowledge and result in quantitative targets (Villard and Jonsson, 2009). Over the last few decades, our appreciation of the role of saproxylic life in evidence-based conservation has increased substantially. As a result, dead wood ecology has grown as a discipline and its potential to address a broad range of general biological questions has been recognized (Stokland *et al.*, 2012; Ulyshen and Šobotník, 2018). However, much remains to be learned about the basic taxonomy and faunal distribution of saproxylic organisms, the functioning of saproxylic ecosystems and the impacts of forest management and global climate change on saproxylic biodiversity. Based on the contributions of this thesis to these questions, I propose the following steps for further related research.

Functional-trait-based approaches have become a well-accepted strategy in community ecology research, with several advantages compared to purely species-based approaches (McGill *et al.*, 2006). The use of functional traits provides mechanistic insights into community functioning and assembly processes and allows a generalization across scales (McGill *et al.*, 2006; Carmona *et al.*, 2016; Albrecht *et al.*, 2018). The first article of this thesis provides one example of a trait-based approach to saproxylic species (further examples: Gossner *et al.*, 2013; Bässler *et al.*, 2014; Seibold *et al.*, 2015; Thorn, Förster, *et al.*, 2018). Trait-based approaches rely on the availability of standardized measured traits for the studied species community. However, in the case of saproxylic beetles most studies of functional traits have been based on traits extracted from the literature, with a focus on ecological traits (e.g., decay niche, wood diameter niche, canopy niche; see Section 3.2.1) and therefore on established niches in dead wood as a habitat. Earlier reports on the ecological traits of beetles are the work of a few coleopterists, based on their lifelong expertise and extended sampling (Freude *et al.*, 1983; Köhler, 2000; Schmidl and Bussler, 2004; Möller, 2009). Nonetheless, studies of ecological traits may be biased by their selectivity (e.g., personal study area of the expert) and may therefore not be replicable or

applicable to other species in further studies. Instead, morphological traits (i.e., traits measurable at the species level) have the advantage of being measurable using standardized protocols (Moretti *et al.*, 2017; Dawson *et al.*, 2019). However, with the exception of body size (Freude *et al.*, 1983), studies of morphological traits and a standardized protocol for saproxylic beetles are lacking. Therefore, I initiated a framework with which to compile a morphological trait database of saproxylic beetles, focusing on species of Central Europe (Figure 5). The measurement protocol consists of 47 morphological traits per species, including body size and shape (body length, body height, elytra length), locomotion (wing area, leg length), foraging (in-lever length, jar length) and sensory organs (eye area, antenna length, hairiness). The saproxylic trait database provides a standardized resource that can be combined with sampled community data from survey and experimental studies to obtain mechanistic insights into community functioning and assembly processes and to allow generalization across scales.

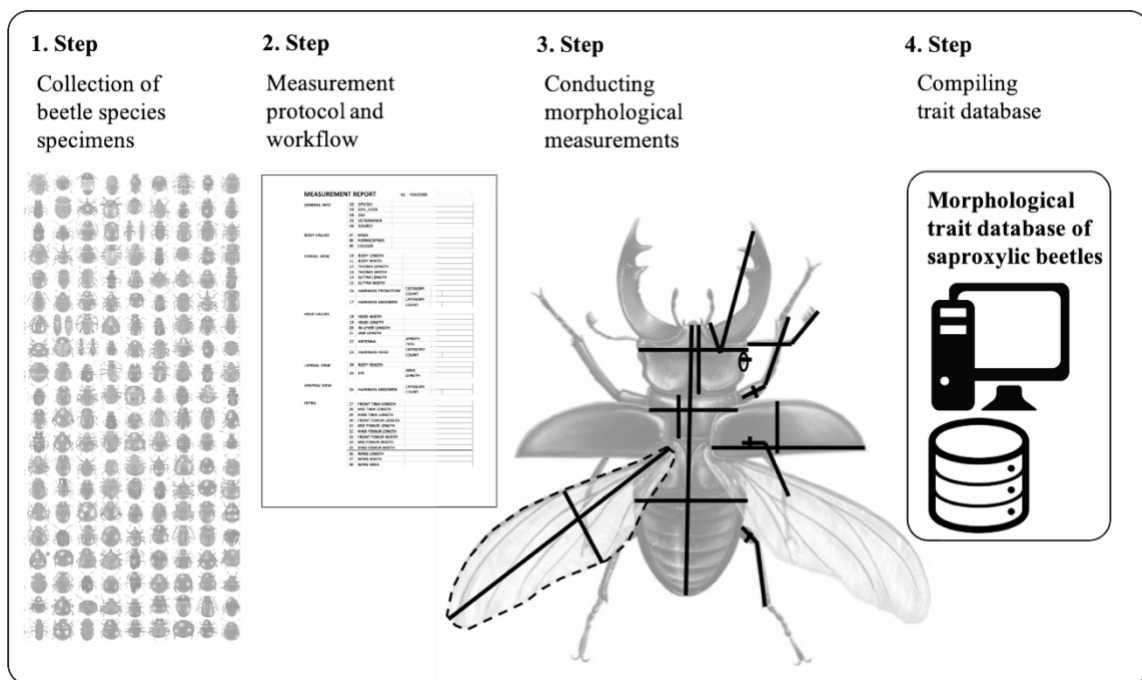


Figure 5: A framework for the compilation of a morphological trait database of saproxylic beetles.

Key aspects of saproxylic biodiversity are characteristics related to dead wood diversity and habitat configuration (Fahrig, 2013; Seibold, Bässler, Brandl, *et al.*, 2016; Seibold *et al.*, 2017). The vertical dead wood experiment of Article III showed that the vertical axis in forest is an important factor for dead wood diversity and that differences in the amount of solar radiation along the gradient from the forest floor to the canopy best explained this

diversity. To further distinguish between the roles of the vertical stratum of dead branches and sun exposure, I conducted an experiment comparing beetle assemblages along vertical and horizontal gradients of sun exposure (Figure 6). Bundles of branches were exposed along a vertical gradient (near the forest floor, lower canopy, upper canopy) and a gradient of sun exposure (completely shaded, half shaded and sun-exposed). Because the effects of vertical dead wood position and sun exposure may differ depending on the tree species, the sampling of saproxylic species was separated by tree species.

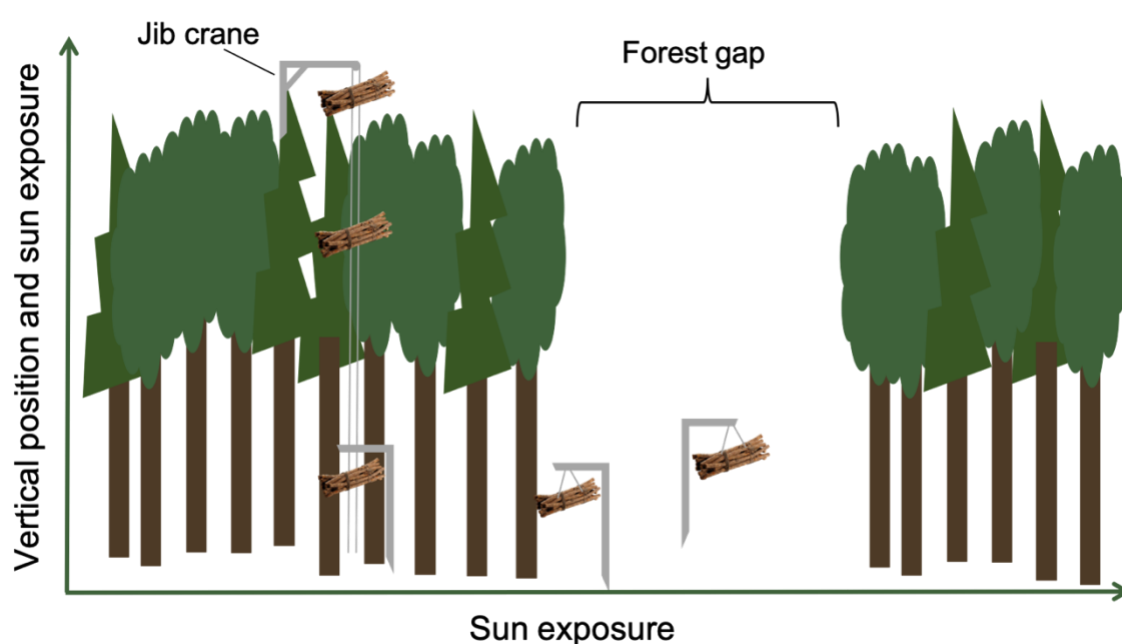


Figure 6: Experimental design of the extended vertical dead wood experiment to distinguish the contributions of vertical position and sun exposure in saproxylic biodiversity.

Coarse woody debris is a particularly important habitat of saproxylic organisms (Siitonen, 2001), especially for threatened species (Seibold *et al.*, 2015). However, the effects of the horizontal and vertical positions of coarse woody debris and their interaction with the microclimate have yet to be investigated. In the framework of the BioHolz project (www.bioholz-projekt.de), I established an experimental approach to disentangle the roles of spatial arrangement and dead wood structure as determinants of saproxylic biodiversity (Figure 7). In addition to providing a deeper understanding of the ecological factors affecting saproxylic biodiversity and assembly processes, the results of this experiment will contribute to the development of practical guidelines for active dead wood restoration in forests (Ranius *et al.*, 2014). Each treatment can be interpreted as a potential management

option for the restoration of dead wood. In Europe, the majority of forest are currently of intermediate age, with old stands (>120 years) covering < 8% of the total forest area (Vilén *et al.*, 2012). Terminal and decay stages are largely absent and senescence is never realized, as most forests are harvested before the trees reach old age (Faustmann, 2003). This is also true for most protected forest areas in Europe. Therefore, active restoration management options (Figure 7) could be enacted to provide dead wood continuity, until European forests reach their natural terminal and decay stages and dead wood formation via senescence occurs.

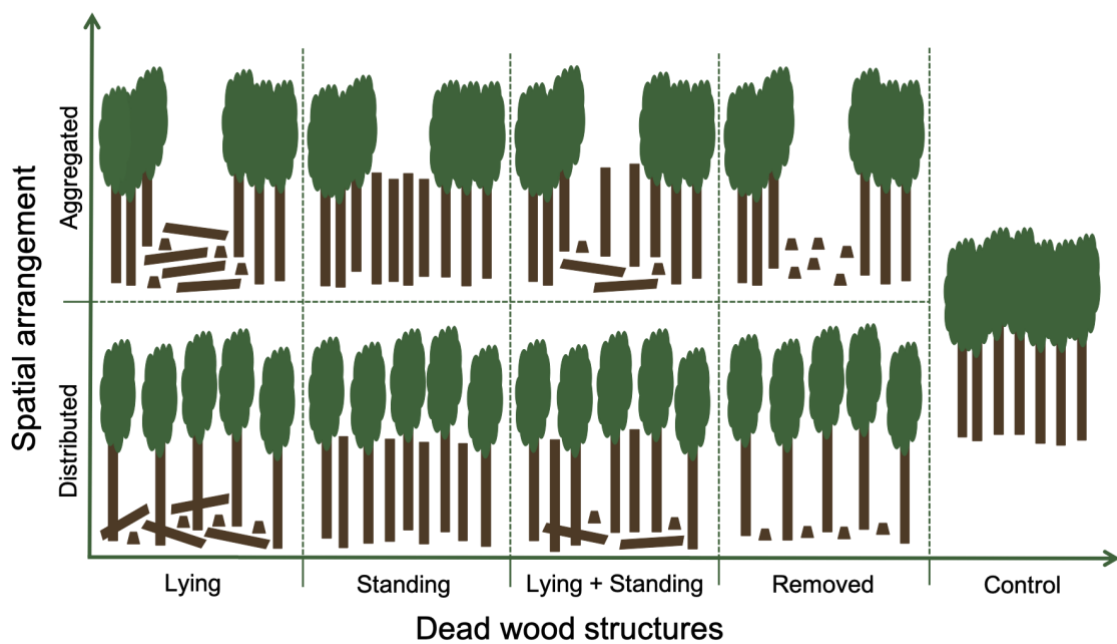


Figure 7: Experimental design within the framework of the BioHolz project. The aim of the experiment is to disentangle the effects of the horizontal and vertical distribution of dead wood and coarse woody debris on saproxylic biodiversity.

In an international cooperation, I was part of a group interested in the drivers of population eruptions and especially the causes underlying the collapse of *I. typographus* populations, which are still not fully understood (Biedermann *et al.*, 2019). However, this knowledge is essential for pest control. Thus, further research should integrate the many drivers governing the bark beetle system (Biedermann *et al.*, 2019). The demonstrated efficacy of bark-gouging for bark beetle control in protected areas, discussed in this thesis, should be implemented and further developed. For example, the development of harvester heads for bark gouging will allow the use of bark gouging to control large-scale outbreaks. Further research should also focus on the applicability of bark gouging as a control measure of bark

beetle pest species with an ecology similar to that of *I. typographus*, namely *Dendroctonus ponderosae* Hopkins, 1902 (North America), *Dendroctonus frontalis* Zimmermann, 1868 (Central America), and *Dendroctonus rufipennis* Kirby (Central and North America). A better understanding of the function of bark in bark beetle colonization and in control processes may also derive from investigations of the effect of bark cover on the profile of volatile chemicals emitted from dead wood. These chemicals differ between tree species and change over the course of decomposition (Holighaus, 2012). Saproxylic beetles are able to differentiate between the different chemical profiles to locate new dead wood resources (Weissbecker *et al.*, 2004; Holighaus, 2012).

5.8 Conclusion

Biogeographical history, climate and anthropogenic processes are drivers of the large-scale patterns of saproxylic biodiversity. Today, forests in Europe reflect deforestation, a forest management optimized for wood production and the absence of old-growth structures, particularly the diversity and amount of dead wood. Land-use intensification threatens saproxylic biodiversity, as anthropogenic habitats exploited for forestry and agriculture do not support species conservation. Integrative forest management strategies that take into account the multiple functions of forests will preserve biodiversity. These strategies must include the retention of old-growth forest elements, the maintenance of natural processes of dead wood creation and active dead wood restoration during logging activities. The vertical and horizontal diversity of dead wood in forest ecosystems drives saproxylic biodiversity and ecosystem functioning. This was demonstrated by the placement of dead branches in the upper canopy, which increased dead wood diversity and correlated positively with saproxylic biodiversity. Dead wood retained on the forest floor has the additional benefit of protecting saplings from the browsing of roe deer. The active removal of dead wood in the management of natural disturbances and in the pest control of bark beetles should be avoided, replaced by on-site bark gouging, especially in protected areas when non-intervention is not an option. The additional advantages of bark gouging include biodiversity protection, economic savings and a positive public perception of forests. Today, there is a very large demand for novel approaches to forest conservation, both by practitioners and political decision-makers. The results of this thesis are an important contribution to meeting this demand.

6 References

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Zobel, M. (2016) The species pool concept as a framework for studying patterns of plant diversity. *J. Veg. Sci.* **27**: 8–18.

Appendix A – Curriculum Vitae

Personal data

Jonas Hagge

Birth: 18.02.1990 in Hamburg, Germany

Privat address: Vimystr. 4, 85354 Freising

Email: jonashagge@posteo.de

Telephone: +49-151-14448079

Education

2016 – 2019 **PhD student** at the Technical University of Munich (TUM) in the framework of the BioHolz project in cooperation with the Bavarian Forest National Park

2015 – 2019 **Master of Science - Environmental Geography: Systems, Processes, and Interactions**, Philipps-Universität Marburg

Thesis: Forest structure and temperature drive colour lightness of beetles

Grade: 1.0

2013 – 2016 **Master of Science - Biodiversity and Conservation**, Philipps-Universität Marburg

Thesis: The *Carabus waga*e complex: phylogeography of a trans-Tibetan ground beetle species group

Grade: 1.0

2010 – 2013 **Bachelor of Science - Biology**, Philipps-Universität Marburg

Thesis: Migratory behaviour determines avian fruit colour preferences

Grade: 1.3

2000 – 2009 **Abitur** at Lauenburgische Gelehrtenschule Ratzeburg

Grade: 2.0

Professional experiences

1/2019 – today Member of scientific staff of Bavarian Forest National Park, Germany

- Research coordination and fieldwork in different dead wood experiments
- 5/2016 – today Scientific staff at the Department of Animal Sciences, Chair of Zoology, Entomology working group, Technical University of Munich, Germany
- Scientific staff in the BioHolz project: researching biodiversity and ecosystem services of forests to support the implementation of the German National Biodiversity Strategy (German Federal Ministry for Education and Research, no. 01LC1323A)
- 2011 – today Freelance consultant for ornithology, bats, dragonflies and ground beetles
- 2009 – 2010 Civil service in the Schleswig-Holstein Wadden Sea National Park, NABU Naturzentrum Katinger Watt
- Environmental education, conservation management, monitoring

Reviewer since

- 2019 Biodiversity and Conservation
- 2019 Ecology and Evolution
- 2018 Forest Ecology and Management
- 2018 Insect Conservation and Diversity
- 2017 European Journal of Forest Research

Appendix B – Publication list

Publication list of the six articles include in this thesis.

Published

Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H., Christensen, M., Gossner, M. M., Heilmann-Clausen, J., Horak, J., Gruppe, A., Isacson, G., Köhler, F., Lachat, T., Larrieu, L., Schlaghamersky, J., Thorn, S., Zapponi, L., & Müller, J. (2019). Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *Journal of Biogeography*, **46**, 1054–1065. <https://doi.org/10.1111/jbi.13556>

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* These authors contributed equally to this study.

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