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Lehrstuhl für Terrestrische Ökologie

# **Biodiversity conservation in temperate European forests: the roles of management intensity and tree species composition**

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## Zusammenfassung

Wälder sind wichtige Ökosysteme, die annähernd ein Drittel der Landmasse des europäischen Kontinents ausmachen. Aufgrund ihrer hohen strukturellen Komplexität und der Vielfalt existierender Baumartengesellschaften, die an ein breites Spektrum möglicher Habitattypen und klimatischer Bedingungen angepasst sind, sind Wälder Lebensräume für zahlreiche Lebewesen. Der Großteil der europäischen Wälder blickt auf eine lange Geschichte menschlicher Nutzung zurück, und auch heute unterliegen sie verschiedensten Formen der Bewirtschaftung. Diese reichen von intensiver Forstwirtschaft mit gleichaltrigen Monokulturen wirtschaftlich rentabler Baumarten bis hin zu Nationalparks und Naturwaldreservaten, in denen Eingriffe ausgeschlossen sind. Dazwischen wird mit Ansätzen integrativer Waldbewirtschaftung versucht, multifunktionale Bestände zu schaffen, die sowohl die Nutzung der Ressource Wald als auch die Erhaltung von ökologischen Funktionen und der biologischen Vielfalt auf gleicher Fläche ermöglichen. Waldbauliche Entscheidungen steuern wesentliche Eigenschaften von Wäldern, insbesondere die Baumartenzusammensetzung, die Vorratshaltung, die Altersstruktur der Bestände und die Menge ökologisch relevanter Strukturen wie Totholz und Habitatbäume. Mit diesen Entscheidungen beeinflusst Waldbewirtschaftung, entweder direkt oder durch Veränderungen in der Waldstruktur, die Biodiversität und die Artenzusammensetzung der in den Wäldern beheimateten Lebensgemeinschaften.

Die vorliegende Arbeit trägt zum Verständnis der Auswirkungen von Waldbewirtschaftung auf die biologische Vielfalt bei, indem die Effekte von Bewirtschaftungsintensität und Baumartenzusammensetzung, zwei wesentlichen Elementen des forstlichen Managements, auf eine Reihe von Artengruppen unterschiedlicher trophischer Ebenen untersucht werden. Die Grundlage der Analysen bilden zwei Datensätze aus vier mitteleuropäischen Regionen mit insgesamt 187 Untersuchungsflächen. Die Bewirtschaftungsformen der Wälder reichten vom vollständigen Ausschluss forstlicher Eingriffe bis hin zu intensiv genutzten Altersklassenwäldern einer einzigen Baumart. Während alle Untersuchungsgebiete natürlicherweise von Rotbuche (*Fagus sylvatica*) dominiert wären, bestanden die Wälder auf den Untersuchungsflächen neben reinen Buchenbeständen auch aus forstwirtschaftlich bedeutsamen Baumarten wie der Eiche (*Quercus spp.*), der Kiefer (*Pinus sylvestris*) und der Fichte (*Picea abies*). Teilweise befanden sich diese Baumarten außerhalb ihres natürlichen Verbreitungsgebietes. In einer ersten Analyse habe ich untersucht, wie sich Bewirtschaftungsintensität, das Altersstadium und die dominierende Baumart auf herbivore

Insekten in der Kronenschicht und in Bodennähe auswirkten. Alle drei betrachteten Elemente prägten die Artenzusammensetzung und beeinflussten die Abundanz und die Artenzahl pflanzenfressender Insekten. Jedoch hingen diese Effekte stark von den Ernährungsgewohnheiten der Insekten sowie von der untersuchten Schicht des Waldes ab. In einer zweiten Analyse wurde untersucht, wie sich die Beimischung einzelner Baumarten wie Eiche, Kiefer und Fichte zu ansonsten buchendominierten Beständen auf Pflanzen, Pilze, Arthropoden, Vögel und Fledermäuse auswirkt. Während die Unterschiede in der lokalen Artenvielfalt eher gering ausfielen, veränderte die Beimischung von Baumarten häufig die Artenzusammensetzung und erhöhte die Artenvielfalt auf Landschaftsebene (Gamma-Diversität) für viele der untersuchten Artengruppen. In einer dritten Studie konnte ich zeigen, dass junge Naturwaldreservate einen Beitrag zum Schutz der Artenvielfalt leisten, auch wenn sie auf eine lange Nutzungsgeschichte zurückblicken und eingebettet sind in eine Landschaft von mit einem integrativen Managementkonzept schonend bewirtschafteten Beständen. Da Naturwaldreservate häufig in Beständen ausgewiesen werden, die sich in der Optimalphase der Waldentwicklung befinden und daher noch keine altersbedingte Seneszenz aufweisen, ähnelten sie strukturell noch bewirtschafteten Wäldern. Trotzdem beherbergten Naturwaldreservate teilweise andere Arten und begünstigten das Vorkommen von Fledermäusen und Vögeln, während Pflanzen und Käfer von einer erhöhten Lichtverfügbarkeit in bewirtschafteten Beständen profitierten.

Die Ergebnisse dieser Arbeit zeigen, dass die Bewirtschaftung der Wälder die Artengemeinschaften verschiedener trophischer Ebenen stark prägt. Dabei wirken sich einzelne Elemente der Bewirtschaftung unterschiedlich auf die verschiedenen Artengruppen aus. Einige der Effekte können durch Veränderungen in der Totholzverfügbarkeit, den Lichtverhältnissen oder mit der Häufigkeit bestimmter Habitatstrukturen erklärt werden, was die Bedeutung dieser Faktoren für die Artenvielfalt in Waldökosystemen unterstreicht. Auch die vollständige Einstellung der Bewirtschaftung trägt zum Schutz der Artenvielfalt bei, und der Wert von Naturwaldreservaten für den Naturschutz wird mit dem Eintritt der Bestände in späte Sukzessionsstadien weiter zunehmen. Die Zusammensetzung der Baumschicht erweist sich als ein Schlüsselfaktor für alle untersuchten Artengruppen. Viele Arten sind an bestimmte Baumartenmischungen gebunden, insbesondere die Gattungen *Quercus* und *Pinus* weisen eine große Zahl von Spezialisten auf. Während auch Buchenwälder eigene und schützenswerte Artengemeinschaften beherbergen, kann die Beimischung anderer Baumarten die strukturelle Heterogenität und die biologische Vielfalt auf Landschaftsebene steigern. Die Forstwirtschaft kann folglich mit der Förderung von Totholzanreicherung,



Habitatbäumen und kleinräumigen Störungen für verbesserte Lichtverfügbarkeit, und durch die Einbeziehung strukturreicher Bestände in der Ausweisung von Naturwaldreservaten einen Beitrag zum Naturschutz leisten. Mit Wäldern die sowohl Bestände natürlicher Baumartenzusammensetzungen als auch solche mit beigemischten Baumarten enthalten, fördert integrative Bewirtschaftung die Artenvielfalt im Wald.



## Summary

Forests are important ecosystems that today cover almost a third of Europe's terrestrial surface. Due to their high structural complexity and the diversity of existing tree species communities adapted to a broad spectrum of habitat features and climatic conditions, forests provide habitats for a large number of plant and animal species. The overwhelming majority of European forests have long histories of anthropogenic land use, and today's forest landscapes are subject to a variety of management approaches. These range from intensive forestry in the form of even-aged monocultures of economically profitable tree species to the exclusion of management in national parks and forest reserves. Integrative management approaches attempt to create multifunctional stands that reconcile resource production and the maintenance of ecological functions and biodiversity. Forest management controls key properties of forest ecosystems, the most important of which are a stand's tree species composition, tree density, age structure, and the accumulation of conservation-relevant structures like dead wood and tree-related habitat structures. These management decisions are known to, either through direct effects or mediated by changes in forest structure, influence the biodiversity and the community composition of the plant, fungal and animal communities hosted by the forests.

This thesis contributes to the evaluation of forest management effects on biodiversity by investigating the impacts of overall management intensity and tree species composition, two integral elements of forest management, on a series of taxa covering several trophic levels. The analyses were based on two datasets from Central European forests that included a total of 187 research plots in four geographical regions. Studied forests were subject to different management approaches ranging from the complete exclusion of management interventions to intensive age-class forests of a single tree species. While forests in all study regions would be naturally dominated by European beech (*Fagus sylvatica*), next to pure beech forests they also included stands dominated by economically relevant tree species like oak (*Quercus spp.*), Scots pine (*Pinus silvestris*), or Norway spruce (*Picea abies*), planted at least in part outside their natural ranges. In a first analysis, I investigated how management intensity, stand developmental stage and the identity of the dominating tree species impacted herbivorous insects in the canopy and the understory. All three elements of forest management shaped community composition and affected abundances and species richness of herbivorous insects, but responses strongly depended on the preferred feeding habits of the herbivores and on the stratum of the forest they inhabit. In a second analysis, I more

closely examined the impact of tree species composition on biodiversity by investigating effects of single-species admixtures of oak, pine and spruce to mature, beech-dominated forests on plants, fungi, arthropods, birds and bats. While effects on plot-level biodiversity were weak, the admixture of tree species often significantly altered community composition and increased landscape-scale diversity. In a third analysis, I showed that recently established strict forest reserves, with a history of forest management and located in a landscape of forest under progressive integrative management, contribute to the conservation of biodiversity. Despite preserving structural characteristics of managed forests and often comprising mature stands in the optimum phases of development without small-scale disturbances and natural senescence, strict forest reserves hosted partly different species and benefitted bats and birds whereas increased light availability in managed stands benefitted plants and beetles.

The findings in this thesis emphasize that forest management strongly shapes communities of forest taxa across different trophic levels, with individual management aspects often benefiting some species while disadvantaging others. Some effects were driven by deadwood, light availability, and the presence of tree-related microhabitats, confirming their relevance for forest biodiversity. Complete cessation of management also contributes to biodiversity conservation, and the value of strict forest reserves will likely increase as they enter late-successional developmental stages. Tree species identity was proven to be a key factor for all surveyed taxa, with many specialist species associated with particular tree species mixtures and confirming the importance of genera *Quercus* and *Pinus* for the conservation of forest biodiversity. While beech forests also host unique communities, the admixture of other tree species can significantly increase habitat heterogeneity and landscape-level biodiversity. Forest management could thus support the conservation of forest biodiversity by continuing to promote key features like deadwood, habitat trees, and increased light availability through small-scale disturbances, and by including more structurally rich stands in the designation of new forest reserves. By creating forest landscapes that include a variety of admixed tree species as well as stands with a natural tree species composition, integrative forest management will benefit overall forest biodiversity.

# 1. Introduction

## 1.1. Temperate forests of Central Europe

Central Europe belongs to the northern temperate zone, with oceanic influences in the west and a more continental east characterized by lower humidity and higher temperature variation. In this region, usually defined as reaching from southern Sweden to the Italian Alps and from eastern France to Poland, forests are the main potential natural habitat in most landscapes below the tree line and would be covering most of the terrestrial landmass in the absence of anthropogenic land-use changes (Leuschner and Ellenberg, 2017). The length of the growing season in this climate favors deciduous broadleaved species such as European beech (*Fagus sylvatica*; henceforth ‘beech’) and pedunculate oak (*Quercus robur*). Yet, woody vegetation is assumed to have been almost completely eradicated in Europe during the ice ages, with only a few refugial habitats remaining (Demesure et al., 1996; Magri, 2008). This made recolonization arduous and is the reason for a relatively poor contemporary diversity of tree genera compared to North America and East Asia (Lang, 1994). One of the most recent tree species to recolonize Europe after the last ice age was beech, but it quickly rose to dominate the natural vegetation at a wide range of site conditions and has been doing so for the last four millennia (Leuschner and Ellenberg, 2017).

The majority of Central European broadleaved forests can be classified as hardwood broadleaved forests of the order Fagetalia sylvaticae, dominated by the genera *Acer*, *Fagus*, *Fraxinus*, *Tilia* and *Ulmus* (Leuschner and Ellenberg, 2017). Of these, forests dominated by beech are by far the most extensive, and characteristic of Central Europe. The tree species composition of forests is determined as much by the between-species competition for light, water, and other resources, as it is a function of inherent physiological ranges. The shade-tolerant and shade-producing European beech outcompetes other tree species on most soils and only loses its advantage at the extremes of ranges of nutrient and water availability, with

its realized niche coming close to its physiological range (Leuschner and Ellenberg, 2017). On a wide spectrum of soil chemical and physical characteristics as well as climatic conditions, the late-successional beech dominates stands by producing deep shade while simultaneously regenerating quickly despite the low light availability, successfully outcompeting other tree species for canopy space. This is possible by adaptations in beech leaves that allow for the efficient use of even fleeting flecks of sunlight for photosynthesis (Küppers and Schneider, 1993). In the absence of anthropogenic land use, beech would come to dominate almost two-thirds of the terrestrial area of Central Europe (Bohn and Gollub, 2007). While beech dominates forest communities in its physiological optimum, most other tree species are relegated to occupy ecological niches in suboptimal soil and climatic conditions. Oak (*Quercus spp.*; henceforth ‘oak’) claims the place of second most important broadleaved forest tree in Central Europe with the pedunculate oak (*Quercus robur*) and the sessile oak (*Quercus petraea*). Oaks require higher light intensities to successfully regenerate (Annighöfer et al., 2015), and the relatively open canopies of oak forests are therefore often rich in other tree species. Outcompeted by beech in many habitats, they thrive as thermophilic mixed oak forests on very dry or as moist mixed oak forests on very wet soils (Leuschner and Ellenberg, 2017).

Due to the wide geographical and ecological amplitude of beech forests, a large variety of different beech forest associations has been described. Only *Galium odoratum*, *Festuca altissima*, *Neottia nidus-avis*, *Dentaria bulbifera* and *Prenanthes purpurea* (Leuschner and Ellenberg, 2017) are named as character plant species for beech-dominated forests in general, and even they are not ubiquitous. Thus, the associated diversity of beech-dominated forests varies greatly, with very species-rich and productive types such as the Galio odorati-Fagetum on moderately base-rich and fairly nutrient-rich soils with a high water storage capacity on one hand, and especially species-poor Luzulo-Fagetum communities on acidic soils in submontane areas on the other (Leuschner and Ellenberg, 2017). In the latter, the herb layer is often lacking completely. This substrate-dependent difference in associated biodiversity has been explained by the fact that most refugia during the last ice age were located on calcareous soils (Ewald, 2003). Additionally, the number of associated plant species decreases with increasing distance from the glacial refugia (Willner et al., 2009). In Central Europe, there are around 50 vascular plant species that are considered to be strongly associated with beech forests (Walentowski et al., 2010). Oak forests on the other hand, often in association with hornbeam (*Carpinus betulus*), usually support a more species-rich vegetation both in the tree layers and in the understory (Leuschner and Ellenberg, 2017).

## 1.2. A short history of forest management

In addition to physiological ranges, competitiveness has shaped the tree species composition of natural forest communities in Central Europe. Humans have taken advantage of this by altering competitive interactions to promote tree species of their preference, resulting in forests with tree species compositions that are vastly different from the potential natural vegetation. The anthropogenic shaping of European forests began as early as with the emergence of the first settlements. For a long time, forest resources were exploited without regulation, with large areas being cleared for agriculture and livestock grazing. Increasing population densities and technological advancements led to intense deforestations in the middle ages (Röhrig et al., 2019) and finally to the greatest extent of forest clearance with the onset of the modern era (Ludemann, 2007). Growing concerns about the dwindling resources finally triggered the creation of forest administrations and planned forestry techniques to secure the supply of timber and increase productivity. Deforested areas were being replanted, often with tree species like Scots pine (*Pinus sylvestris*; henceforth ‘pine’) and Norway spruce (*Picea abies*; henceforth ‘spruce’) that offered decent growth rates on the nutrient-depleted soils and were able to handle the missing canopy cover (Röhrig et al., 2019). In some regions, alternating phases of deforestation, abandonment, and reforestation have produced a complex pattern of differently aged forest patches (Hermy and Verheyen, 2007). The emerging modern systems were focused on productivity and, largely replacing coppicing forestry and woodland pastures, gave way to a new era of high forest management (Farrell et al., 2000) that remains the predominant form of forest management today (Spiecker, 2003). Primary and old-growth forests without management interventions are characterized by heterogeneous stands with an uneven age structure including very old trees, small-scale natural disturbances induced by tree senescence or storms, and a continuous forest cover. The high forest systems, on the other hand, are often secondary forests with uniform stands of even-aged trees, frequently consisting of a single tree species (Bauhus et al., 2009). These production forests were often harvested by clear-cutting, i.e. the felling of entire forest sections, before a more recent shift of silvicultural systems to shelterwood cutting. Under both practices, forests are made up of age-class stands in which trees reach only a fraction of their potential natural lifespan. This leads to forest landscapes in which late successional stages, such as the terminal and decay stages, are rare (Hilmers et al., 2018) and where even early regeneration phases are often artificially shortened (Swanson et al., 2011) and characterized by a pronounced structural homogeneity. Consequently, most

managed forests lack structural attributes of old-growth forests like old trees and large amounts of deadwood (Bauhus et al., 2009).

The promotion of fast-growing species like spruce and pine after the emergence of modern forestry lasted until the end of the twentieth century, and thus their distributions and abundances in today's Central European forest landscape far exceed their natural ranges. In Germany, spruce is now the dominating tree species, occupying 25 % of the forest area and followed by pine with 22 % (BMEL, 2014), at the expense of beech (15 %). Oak was a popular tree species even in early forestry systems like wood pastures and coppicing. This led to an increase in oak that was strengthened in the 19<sup>th</sup> century by the efforts of scientific forestry to develop oak high forests for the production of high-quality timber (Mölder et al., 2019). While oak forests also suffered area loss at the hand of the expansion of conifers, they still make up 10 % of the forest area (BMEL, 2014). The exact role of various types of oak forests in the potential natural vegetation of Central European forests, however, remains controversial (Mölder et al., 2019).

Today, forests cover roughly a third of Europe's terrestrial surface (San-Miguel-Ayanz et al., 2015). While this is less than the natural extent of forests in this region, the forested area has been steadily increasing over the past decades (Keenan et al., 2015). In addition to the cultural and economic importance and the value for recreation and human health of forests in general, this underscores their key role for the conservation of biological diversity in Europe. While forest management has been mostly focused on the supply of timber in the past, a more differentiated view of forest ecosystems has gained importance in the last decades, calling for forest management practices that live up to the multifunctional role of forest ecosystems (Lindenmayer et al., 2012).

### **1.3. Sustainable forest management**

While forests are indispensable as sources of primary materials, the prioritization of resource production led to the establishment of management practices that disregard other forest functions. In addition to timber, forests provide a number of ecosystem services that are less easily quantified. Among others, they serve as important carbon stocks, stabilize soils, play a role in hydrological regulation and the provision of drinking water, and have important cultural and recreational value (Alcamo and Bennett, 2003; Costanza et al., 1997). They also host a large part of the planet's biodiversity (Lindenmayer and Franklin, 2010). These functions and services have often been impaired by traditional management approaches, while susceptibility to biotic and abiotic damage was increased (Jactel et al., 2009). The idea



of sustainable forestry was introduced as early as at the beginning of the 18<sup>th</sup> century by von Carlowitz and expanded to include ecological issues by the end of the 19<sup>th</sup> century (Gayer, 1886). But it took another century for the ideas of multifunctional forests to gain traction in European forest policy. In Helsinki in 1993, the Ministerial Conference on the Protection of Forests in Europe reflected Europe's intention to adhere to the decisions of the United Nations Conference on Environment and Development (UNCED). The resolutions of the Helsinki conference contained commitments to sustainable forest management, the conservation of biological diversity, and strategies regarding climate change (Mayer, 2000). This also included reaching an agreement on the definition of sustainable forest management as "the stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfill, now and in the future, relevant ecological, economic and social functions, at local, national, and global levels, and that does not cause damage to other ecosystems" (Second Ministerial Conference on the Protection of Forests in Europe, 1993). For Central Europe, this meant a transition from the dominating form of forest management, age-class monocultures of economically profitable tree species outside their natural ranges, to stands with a more natural tree species composition, higher amounts of deadwood, preservation of habitat trees, and harvesting regimes that guarantee continuous cover forestry (Spiecker, 2003). Environmental issues and catastrophic weather events in the last decades of the 20<sup>th</sup> century as well as an extreme drought in 2003 emphasized the need for a paradigm change and accelerated the transition to mixed-species stands. Single-species stands in the German state of Baden-Württemberg, for example, decreased from 53 % of the forest area in 1987 to 39 % in 2012 (Pretzsch et al., 2017) and Europe-wide data confirms a steady transition towards mixed stands (Forest Europe, 2015). Following the resolution, many countries integrated the definition of sustainable forest management and the specified guidelines into their national legislations (Rametsteiner and Mayer, 2004).

#### **1.4. Effects of forest management on biodiversity**

Due to their high structural complexity and the diversity of phytosociological associations adapted to a large spectrum of habitat features and climatic conditions, forests provide habitats for a large variety of plant and animal species. Land-use changes and increasing land-use intensity, the main drivers of global biodiversity loss, also threaten forest taxa (Sala et al., 2000). In the past decade, the diversity of arthropods in forests has shown a significant decline (Seibold et al., 2019), with unknown consequences for ecosystem functioning and

resilience (Cardinale et al., 2006; Soliveres et al., 2016). Modern forestry's narrow focus on resource production has led to drastically altered forest ecosystems, and comparisons of structurally homogeneous high-intensity systems with natural old-growth forests often find significant declines in biodiversity (Siitonen, 2001; Stephens and Wagner, 2007). With scientific research being a main purpose of the implementation of strict forest reserves in Central Europe, a sizable body of literature exists on the effects of forest management intensity on biodiversity in temperate forests. A meta-analysis by Paillet et al. (2010) analyzing multiple taxa found that overall, species richness was higher in unmanaged compared to managed forests. Species dependent on continuous forest cover, deadwood availability, or other characteristics of undisturbed old-growth forests, such as bryophytes, lichens, fungi, and saproxylic insects, were negatively affected by forest management. The pivotal role of primary forests for biodiversity conservation has been confirmed repeatedly, especially for saproxylic species that require the presence of deadwood at least once during their life cycles (Eckelt et al., 2018; Lachat and Müller, 2018; Müller et al., 2007b; Seibold et al., 2015). Differences often become less apparent when considering forest management not as a binary variable but as the range of combinations of forestry tools that exist in Central Europe. Confirming this effect, Chaudhary et al. (2016) showed that regarding local species richness, management regimes can be ranked from the highest species richness in selection and retention systems to the lowest in timber and fuelwood plantations. Negative forest management intensity effects on biodiversity have also been shown for European beech forests, where selectively harvested forests were found to be of higher conservation value for several taxonomic groups than a more traditional shelterwood system (Brunet et al., 2010), although recent studies have shown that these differences can be outweighed by a greater diversity of habitats at the landscape scale (Schall et al., 2018b). Also investigating beech forests, Müller et al. (2007b) showed that deadwood-dependent beetles, fungi, and wood-inhabiting and cavity-nesting birds decline significantly with increasing management intensity among three management categories ranging from traditional high forest management to unmanaged strict forest reserves, with intermediate levels for forests under integrative management. Not only do effects of forest management intensity often weaken when less intensive forms of management are included, but the effects also depend highly on the taxonomic groups that are investigated. While many species reliant on old-growth structures are disadvantaged by forest management, vascular plants often respond positively (Paillet et al., 2010), and some species groups show no reaction at all.

These studies emphasize that forest management decisions impact forest biodiversity, often in similar ways across forest types, regardless of differences in land-use histories and in how forest management policies are implemented locally. To understand which ecological mechanisms link forest management to effects on biodiversity, it is necessary to investigate how management decisions affect the characteristics of forest stands and how these features, in turn, affect biodiversity (Dieler et al., 2017; Müller et al., 2008; Penone et al., 2019). The role of some forest features is well understood, and it has been shown that they can outperform mere management categories when it comes to explaining forest community patterns (Duguid and Ashton, 2013; Gossner et al., 2014b), but many features are strongly correlated, and individual effects and mechanisms remain difficult to untangle (Schall et al., 2018a).

One of the best-known forest features with strong effects on biodiversity is the amount and type of available deadwood. Deadwood is a key resource in the life cycles of many organisms, most importantly fungi and arthropods, but also including mammals, mollusks and birds, among others (Stokland et al., 2012). Different host tree species, decay stages and microclimatic conditions increase the number of ecological niches and thus support a higher diversity of saproxylic species (Blaschke et al., 2009; Floren et al., 2014; Gossner et al., 2016; Seibold et al., 2016; Vogel et al., 2020). Strategies of deadwood enrichment have been shown to significantly increase the diversity of saproxylic fungi and beetles in managed beech forests (Doerfler et al., 2018). But deadwood availability does not only benefit fungi (Bässler et al., 2010; Blaschke et al., 2009) and beetles (Gossner et al., 2013b; Seibold et al., 2017; Seibold and Thorn, 2018), also groups like wood-inhabiting birds (Müller et al., 2007b), soil macro arthropods (Jabin et al., 2004) and snails (Kirchenbaur et al., 2017; Müller et al., 2005a) react positively to deadwood enrichment. Deadwood availability is closely related to another forest feature: The abundance and diversity of microhabitat structures on living and dead trees (Bütler et al., 2013; Larrieu et al., 2018). Tree-related microhabitats like cavities, cracks, or bark features have been shown to have positive effects on a number of taxa including beetles (Bouget et al., 2014b), birds and bats (Paillet et al., 2018). Larger and older trees are more likely to bear relevant microhabitat structures (Paillet et al., 2017), showing that stand age is relevant for biodiversity conservation in forests. Older stands are known to host distinct communities (Jeffries et al., 2006), and Moning and Müller (2009) have shown that the species richness of birds, mollusks and lichens increases with forest age, with biodiversity-relevant age thresholds above usual rotation cycles.

Primary producers are a key component of any ecosystem, and their abundance and diversity shape communities and interactions in a significant way (Price, 2002). One of forest management's key elements is determining the plant species and even individuals that will constitute the tree layer, as this shapes the composition and diversity of resources and habitat niches available to all other trophic levels. Accordingly, many studies have shown that the tree species composition is an important driver of community composition and diversity of forest biodiversity (Cavard et al., 2011). Sobek et al. (2009) showed that increasing tree diversity led to a higher abundance and species richness of true bugs and lately, large-scale studies involving a variety of forest types showed that tree diversity is a key driver of overall forest-associated biodiversity (Ampoorter et al., 2019; Penone et al., 2019). Even the admixture of single trees of different species to otherwise homogeneous stands can have a significant ecological impact on associated biodiversity (Ohsawa, 2007; Wehnert and Wagner, 2019). These effects are often driven by the increased structural heterogeneity of mixed stands (Juchheim et al., 2019), which is why effects increase with the functional diversity of the involved tree species (Ampoorter et al., 2019). Not only the functional groups but also the identity of a tree species have significant effects on the diversity and community composition of several species groups (Penone et al., 2019; Vehviläinen et al., 2007). Finally, forest management influences the light availability in forests through the functional trait space of the tree species and through thinning and harvesting measures that cause small-scale disturbances and changes in canopy cover (Ehbrecht et al., 2017; Ehbrecht et al., 2019). These disturbances often favor vascular plant species in the herb layer (Boch et al., 2013), saproxylic beetles (Bouget et al., 2014b) and other aboveground species groups (Kirchenbaur et al., 2017; Penone et al., 2019), although the positive effects on species richness can be accompanied by a decline in specialization.

Most studies on the effects of forest management on biodiversity conclude that increasing structural heterogeneity at the stand level promotes the diversity of a number of taxa. With their relatively homogeneous stands, this makes age-class forests an unlikely contender for effective biodiversity conservation. Yet, recent studies by Schall et al. (2018b) and Heinrichs et al. (2019) have shown that age-class forests and monocultures can outperform mixed and uneven-aged stands regarding the biodiversity of several taxa, depending on the spatial scale that is observed. Combining stands of different developmental stages or monocultures of different species at the landscape level can maintain typical communities and specialist species while matching or even surpassing the gamma diversity of uneven-aged or mixed forests. Of course, other species yet are associated with continuous forest cover or with

mixed forests and their particular stand structure, relying on the continued existence of stand-scale mixtures. This emphasizes that no single management system can effectively conserve all forest biodiversity (Calladine et al., 2015). For informed policy decisions going forward, it will be vital to understand how and through which mechanisms different management decisions shape forest biodiversity, especially regarding the ongoing transition from monocultures to mixed forests (Felton et al., 2010).

### **1.5. Forest biodiversity conservation**

In the second resolution of the Helsinki conference, the signatory countries committed themselves to the conservation and promotion of forest biodiversity as an essential element of sustainable forest management. Based on this and the simultaneously adopted Habitats Directive of the European Union, governments began developing national concepts for the conservation of biodiversity. This implies the conservation of genetic diversity of populations, species diversity, and the diversity of different ecosystems and their natural processes (BMU, 2007). Central Europe, and especially Germany, occupy a large portion of the natural geographic range of beech forests and accordingly bear responsibility for the preservation of these forests and the associated biodiversity (Knapp et al., 2007). Strategies to conserve biodiversity in forests range from segregative to integrative approaches (Bollmann and Braunisch, 2013). Segregative approaches set aside areas for conservation while optimizing the rest of the forest landscape for the production of resources (Puettmann et al., 2012). Integrative approaches on the other hand aim at balancing economic and ecological functions on the same area by maintaining some structures and processes resembling those of natural forest ecosystems (Bauhus et al., 2013). Integrative approaches are thus especially relevant for the conservation of many communities that profit from traditional forest use. As in the Strategy for Biological Diversity adopted by the German government (BMU, 2007), biodiversity conservation policy often relies on elements of both approaches.

#### **1.5.1. Integrative approaches to biodiversity conservation**

The vast majority of Central European forests are under some form of forest management, reaching values as high as 98 % of the forested area in Germany (Engel et al., 2016). For effective conservation of forest biodiversity, approaches are consequently compelled to include concepts that reconcile biodiversity conservation with commercial uses. The matrix of managed forests not only can support populations, it also plays a role in facilitating the movement of species and in buffering sensitive areas and forest reserves (Lindenmayer and

Franklin, 2010). Integrative management enhances forest biodiversity by preserving or creating old-growth attributes and by pursuing a more natural stand composition. It includes elements such as selective harvesting, maintenance of uneven age structures, natural regeneration, the retention of habitat trees, and deadwood enrichment (Bollmann and Braunisch, 2013). A key element of most integrative approaches in Central Europe is the ongoing transition from coniferous monocultures to mixed forests that more closely resemble the potential natural vegetation (Knoke et al., 2008).

#### 1.5.2. Segregative approaches to biodiversity conservation

While the total forest area in Europe is steadily increasing, the amount of pristine primary forests is small. Almost all forests have a long history of anthropogenic land use, often including periods of non-forest cover. Less than 1 % of European forests are naturally regenerated primary forests without signs of human activities and with intact ecological processes (Sabatini et al., 2018). These forests are often the last refugia for species dependent on old-growth structures and long habitat continuity (Lachat and Müller, 2018), but less than half possess strict formal protection status (Sabatini et al., 2018). In Germany, unmanaged forests – in most cases with a long history of anthropogenic influence – comprise 2.3 % of the total forest area (Engel et al., 2016), shy of the stated goal of reaching a share of unmanaged forests of 5 % by 2020 (BMU, 2007). Segregative approaches aid biological conservation by protecting areas of high conservation value. When established in large enough areas like national parks, set-asides can harbor a large diversity of developmental stages with natural dynamics and support minimum viable populations (Bollmann and Braunisch, 2013). Segregative elements at smaller scales have historically been set aside to study natural forest dynamics (Meyer et al., 2011). With limited potential for additional large national parks, strict forest reserves between one and several hundred hectares in size now play an important role in achieving conservation goals. Strict forest reserves are areas with natural forest types that are well-adapted to the site conditions and are large enough to allow natural forest dynamics to occur (Parviainen, 2000), while management is excluded (Bollmann and Braunisch, 2013). Yet, most forest reserves have been subject to management in the past and, although abandonment leads to an increase in old-growth structures, still preserve characteristics of managed stands that will likely take decades to disappear (Paillet et al., 2015).

## 1.6. Overall aims and structure of this thesis

Integrative management concepts have been shaping forestry policy in Central Europe for several decades. However, an evaluation of how individual management practices impact forest biodiversity is often lacking. In a series of three chapters, I investigated the effects of management intensity and tree species composition on the diversity and community composition of a variety of taxa covering several trophic levels. Using a dataset from a long-term biodiversity monitoring project, I first assessed effects of management intensity and the identity of the dominating tree species on herbivorous insects in different forest strata. In the second chapter, I used a dataset of pure beech forests and beech forests with admixed tree species from the Steigerwald region to investigate how tree species admixture of economically relevant species affects a variety of species groups. Another, partly overlapping dataset from the Steigerwald region was used in the third chapter to assess how strict forest reserves contribute to biodiversity conservation in a forest landscape under integrative management. Findings on these relationships are of importance for the further improvement of forest management policies regarding the promotion and conservation of forest biodiversity. The three studies allowed me to address the following research questions:

Question 1: How does forest management intensity affect forest biodiversity?

1.1 How does management intensity as measured by a continuous silvicultural management intensity index (SMI) affect abundance, alpha diversity and community composition of herbivorous insects?

1.2 Do strict forest reserves in beech and beech-oak forests contribute to the conservation of various taxa within a landscape of forest under integrative management?

Question 2: How does tree species composition affect forest biodiversity?

1.1 How does the dominating tree species in mature, managed stands affect the abundance, alpha diversity and community composition of herbivorous insects?

1.2 How does the admixture of tree species in managed beech forests affect the abundance, alpha diversity, gamma diversity and community composition of various taxa?

Question 3: What role do stand structure and tree-related microhabitats play in mediating effects of forest management on forest biodiversity?

- 1.1 How do structurally different developmental stages in intensively managed age-class beech forests differ regarding the abundance, alpha diversity and community composition of herbivorous insects?
- 1.2 Do variables of stand structure and tree-related microhabitats explain the effects of management intensity and tree species composition on the abundance and alpha diversity of various taxa?



## **2. Methods**

The first chapter of this thesis is based on a large dataset from the Biodiversity Exploratories, while chapters two and three are based on data gathered within the scope of the research project "Management of biodiversity in integrative forestry" in the Steigerwald region in 2017 and 2018. Regarding chapter one, I was involved in the statistical analyses but not in the process of data collection. Regarding chapters two and three, I was involved in the conceptualization of the project, data collection and data analysis. See the author contribution paragraphs in the chapter summaries for detailed information on the attribution of individual tasks. In the following, I will introduce the study regions, research plot selection procedures, and data collection methods for both datasets.

### **2.1. Biodiversity Exploratories**

#### 2.1.1. Research area

The Biodiversity Exploratories constitute a large-scale and long-term research infrastructure to study the relationships between land use, biodiversity, and ecosystem processes and functions. The three study regions are distributed over Germany and include the UNESCO Biosphere Reserve Schorfheide-Chorin in the northeast ( $13^{\circ}23'27''$ – $14^{\circ}08'53''$  E;  $52^{\circ}47'25''$ – $53^{\circ}13'26''$  N), the National Park Hainich and surrounding forests in Central Germany ( $10^{\circ}10'24''$ – $10^{\circ}46'45''$  E;  $50^{\circ}56'14''$ – $51^{\circ}22'43''$  N), and the UNESCO Biosphere Reserve Schwäbische Alb in the southwest ( $09^{\circ}10'49''$ – $09^{\circ}35'54''$  E;  $48^{\circ}20'28''$ – $48^{\circ}32'02''$  N). The research plots lay at altitudes between 3–140 m in the Schorfheide-Chorin, between 285–550 m in the Hainich, and 460–860 m a.s.l in the Schwäbische Alb. Mean annual temperatures and mean annual precipitations are, from north to south, 8.0–8.5 °C and 500–600 mm, 6.5–8.0 °C and 500–800 mm, and 6.0–7.0 °C and 700–1000 mm. All environmental conditions fall into the ranges that would naturally lead to landscapes dominated by

European beech. Nonetheless, due to anthropogenic forest management, leading tree species in the regions also include oak, pine and spruce. Each region includes a range of land-use intensities ranging from unmanaged forests to intensively managed age-class monocultures.

#### 2.1.2. Selection of research plots

To select the research plots, a 100 m x 100 m virtual grid was placed over the entire area of each region, and 438–579 forested grid cells were chosen non-randomly, covering the entire ranges of forest management intensity and tree species composition. On each grid cell, Boch et al. (2013) conducted surveys of vegetation and soil, as well as a detailed forest inventory on a circular 500 m<sup>2</sup> area that included tree characteristics like the stem diameter at breast height (DBH, 1.3 m) and the exact locations of all trees with DBH > 7 cm. Regarding management intensity, forests were classified as unmanaged when no forestry operations had been conducted in the last 20–70 years. Forests were considered age-class forests of various developmental stages (thicket, pole wood, timber, timber with regeneration) when they featured a homogeneous tree age distribution and harvesting intervals of 80–120 years. If harvesting was characterized by the selective cutting of single trees, forests were classified as uneven-aged selection forests. All environmental and management intensity information on the grid cells was then used to select 50 100 m x 100 m research plots in each region based on a stratified random sampling procedure. Plots within a region were selected to cover the variation in management intensity, tree species composition, and soil depth as well as exhibiting a homogeneous soil type and vegetation. Plots were also arranged so that a minimum distance of 200 m was kept between the outer edges of any two plots and 100 m to the nearest forest edge. Research plots were representative of a larger forest stand and were not replicated inside these management units. For a more detailed description of the selection of research plots, see Fischer et al. (2010). For the analyses presented in this thesis, suitable subsets for the testing of various hypotheses were chosen that totaled 126 research plots. Subsetting was necessary since not all management intensities, age-classes or tree species occurred in all regions. Unmanaged forests were always mature beech stands, while managed forests included stands either dominated by beech, spruce, pine, or, in the Schorfheide-Chorin region, mixed stands of beech and pine and stands dominated by oak. Due to variation in soil and climatic conditions between regions, pine and pine-beech research plots are exclusive to the Schorfheide-Chorin region, and spruce-dominated stands are restricted to the Schwäbische Alb and Hainich regions. All managed forests included in the subsets consisted of conventional age-class forests with trees of the same age cohort. All

mixed and conifer plots were in timber-stage stands, while pure beech plots included developmental stages "thicket" (< 30 years), "pole wood" (30–50 years), "timber" (> 90 years) and "timber with regeneration" where 10–20 years old beech thickets grow under a timber-stage canopy.

### 2.1.3. Data collection

#### *Insect sampling*

To gather data on herbivorous insects, flight interception traps were installed in three randomly selected subplots within each research plot. Subplots measured 10 m x 10 m and were located in the corners of the 100 m x 100 m research plot. In each subplot, one interception trap was installed in the outer crown area of the calculated vertical center of the canopy layer (Kowalski et al., 2011). A second interception trap was installed in the understory 1.5 m above ground. Flight interception traps consisted of a pair of intersecting transparent plastic boards measuring 40 cm x 60 m and with funnels leading to sampling jars at the bottom and the top (Gossner and Ammer, 2006). Sampling jars contained 3 % CuSO<sub>4</sub> solution with a drop of detergent to reduce surface tension and were emptied five times from May to October 2008. Sampling was repeated on a subset of 31 research plots in all three study regions in the years 2009 and 2010. Catches were transferred to 70 % ethanol and sorted to taxonomic orders or families in the laboratory. After pooling all samples per trap, two of the three samples per plot and forest stratum were chosen randomly to be identified to species-level by taxonomic specialists. Due to the focus on herbivorous insects, only data on herbivorous beetles (Coleoptera), true bugs (Hemiptera: Heteroptera) and cicadas (Hemiptera: Auchenorrhyncha) was used. All herbivorous insects were further classified into guilds according to their main feeding habits during larval and adult stage (Böhme and Lucht, 2005; Nickel, 2003; Wachmann et al., 2004-2012). Guilds were order-specific and included xylophagous and leaf-chewing feeding habits for beetles and plant-sucking feeding habits for Hemiptera.

#### *Forest structure*

Variables regarding plant composition and forest structure were derived from the vegetation survey and forest inventory data gathered by Boch et al. (2013). The forest inventories were conducted in the center of each plot, on circular areas of radius 12.62 m for trees with a diameter at breast height (DBH) larger than 29.9 cm,  $r = 7.98$  m for trees with  $19.9 \text{ cm} < \text{DBH} < 30.0$ , and  $r = 5.64$  m for trees with  $7.0 \text{ cm} < \text{DBH} < 19.9$  cm. Covariates used in the

analyses were the stand biomass (basal area in  $\text{m}^2 \text{ha}^{-1}$ ), living biomass (volume of trees  $> 7$  cm DBH in  $\text{m}^3 \text{ha}^{-1}$ ), tree density (trees  $> 7$  cm DBH per hectare), stand height (90<sup>th</sup> quantile of tree height), and coarse (CWD; length  $> 0.5$  m and diameter  $> 0.2$  m) and fine (FWD; diameter  $> 0.05$  m) woody debris ( $\text{m}^3 \text{ha}^{-1}$ ).

Vegetation surveys were conducted on a 20 m x 20 m subplot in the center of each research plot in spring and summer 2008. After identifying each species, their percentage cover was estimated. Covariates derived from this dataset included the canopy cover as the relative cover of the tree layer (cover of trees  $> 5$  m), the number of vascular plant species and the Shannon plant diversity using the highest cover estimate from the spring and summer surveys for each species.

### *SMI*

To quantify forest management intensity, the silvicultural management intensity indicator (SMI) was developed by Schall and Ammer (2013). This indicator is based on three main features of a given forest stand. These include the tree species, the stand age and the biomass of living and dead wood. Two components make up the indicator: A risk component that models the risk of stand loss as a function of tree species identity and stand age; and a stand density component based on the harvesting regime, stand age and tree species. The SMI has been shown to adequately measure forest management intensity compared to simple structural attributes when exploring the effects of management intensity on biodiversity (Gossner et al., 2014b).

## **2.2. Steigerwald**

### 2.2.1. Research area

#### *Climate and vegetation*

The Steigerwald area is a predominantly forested region in southern Germany that offers relatively little overall variation in abiotic conditions and the advantage of a large, connected forested area that minimizes risks of fragmentation effects. The elevation in this colline to sub-montane region ranges from 300–450 m a.s.l. Situated in the temperate zone at the transition from maritime to continental climate, the mean annual temperature is 7–8 °C and the region receives 600–800 mm of precipitation. On predominantly acidic soils, its forests are naturally dominated by beech (Walentowski et al., 2001), mainly of the associations "Luzulo-Fagetum" and "Galio odorati-Fagetum" (Leuschner and Ellenberg, 2017), but also include some sites of oak-hornbeam communities. The research area largely overlaps with

the Natura 2000 protection area "Buchentäler und Wiesentäler des Nordsteigerwaldes" (Natura 2000 area number 6029-371), designated to protect species and habitats typical of deciduous forests.

#### *History of forest management*

The Steigerwald area has a long history of forest management. Unregulated use of forest resources in the Middle Ages was replaced by coppicing with standards in the 17<sup>th</sup> century, leading to an increased share of oak (Sperber and Regehr, 1983). In the first half of the 19<sup>th</sup> century, significant portions of the region transitioned to high forest management, often maintaining the traditional combination of oak and beech with a focus on high-value timber (Müller, 2005b). Harvesting was predominantly carried out as shelterwood cutting, and in the 1930s the cultivation of spruce started increasing. Management was heterogeneous during and after the Second World War. Only during the 1980s, forestry practices in a portion of the study area started incorporating practices to increase stand naturalness, including natural rejuvenation of broadleaved tree species and less intensive logging operations. Focus on high-value timber in the northern part of the study region implied the elimination of trees with relatively little economic value. These removed individuals were often trees with microhabitat structures like tree cavities or crown deadwood. The reduction in these structures, in turn, led to a reduction in biodiversity (Müller et al., 2007a; Müller et al., 2007b; Müller et al., 2008).

#### *Forestry Department Ebrach*

Forest management of the region was reformed in 2005 with the establishment of the Bavarian state forest company. As a result, forestry operations in the study area were now managed by the local forestry department of Ebrach. The local forestry department is in charge of all forestry operations within its area, implementing the guidelines of the state forest company that are focused on promoting permanent forest cover and selective logging, as well as increasing local tree species diversity using indigenous species like beech, oak, pine and spruce. The forestry department of Ebrach covers 17,000 ha of state forest. Stands are predominantly deciduous, with beech and oak alone accounting for around 60 % of the total area. 27 % is stocked with Norway spruce, Scots pine, and other coniferous tree species. Harvesting is mainly done by single tree harvesting in a shelterwood system, with extraction volumes of 25-60 m<sup>3</sup> ha<sup>-1</sup> every 5-8 years depending on the tree species composition.

### *Biodiversity conservation and protected areas*

The forestry department of Ebrach adheres to the guidelines of the Bavarian state forest company, which in 2006 implemented a policy of integrative forest management with a special focus on the promotion and conservation of beech forests. A progressive deadwood enrichment strategy was introduced in the forestry department in 2006. The retention of both naturally occurring deadwood, as well as harvest remnants in the form of tree crowns and parts of the stems, have led to a marked increase in the amount of deadwood in managed stands (Doerfler et al., 2017). Additionally, up to ten habitat trees per hectare are exempt from harvesting. These habitat trees exhibit certain structural features like tree cavities or damaged bark that make them valuable for biodiversity conservation. A number of small stand-scale areas with above-average densities of habitat trees are also exempt from management interventions. Finally, 2.5 % of the forestry department's area is contained in six strict forest reserves that are mainly made up of beech and mixed beech-oak forests. The number and area of forest reserves have been increased in several steps since 1978, and management may have taken place in parts of the reserves up to the year of designation.

#### 2.2.2. Selection of research plots

##### *Regular forest inventory*

To investigate how the admixture of tree species to otherwise beech-dominated forests impacts forest structure and biodiversity, it was necessary to select research plots of various tree species compositions. I carried out the process of research plot selection with the help of Johanna Kozak and Thomas Schäff. The characteristic pure beech stands of the Steigerwald region served as a baseline, while gradients of tree species admixture were established using mixed stands with increasing proportions of each tree species of interest, i.e. oak, pine and spruce (henceforth 'forest types'). Additionally, research plots had to be established in pure beech stands and mixed beech-oak stands in strict forest reserves in order to be able to investigate effects of forest management intensity and possible interactions with tree species composition on forest structure and biodiversity.

To guarantee a systematic selection process, a protocol of several steps was developed for the selection of research plots. In a first step, data from the regular forest inventory conducted by the Bavarian state forest company was used. These forest inventories are conducted approximately every ten years and collect detailed data on the living stand and dead wood on circular, permanently marked 0.05 ha inventory sites that cover the entire state-owned forest in a regular 200 m x 200 m grid (100 m x 100 m in strict forest reserves). On each

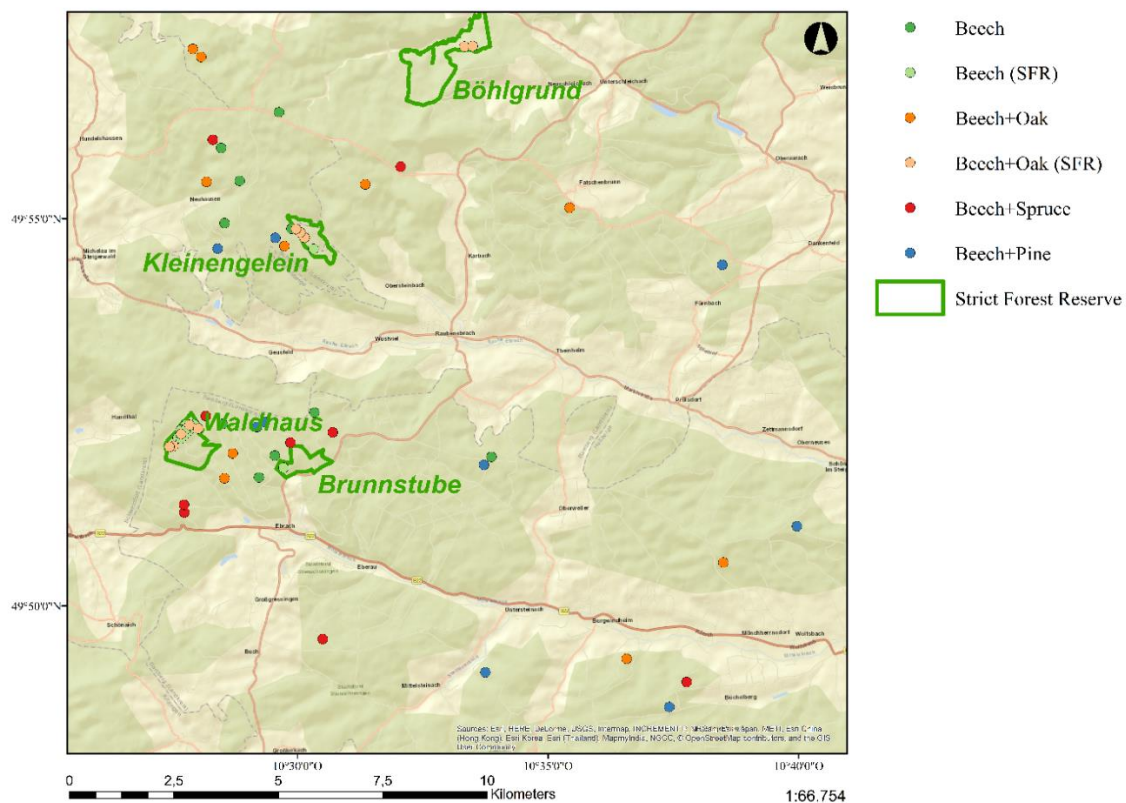
inventory site, the DBH and the location of each tree  $\geq 0.2$  m height are recorded, with different DBH thresholds depending on the distance from the plot center. In the smallest area (radius = 2.82 m), all trees are recorded. In the next biggest area ( $r = 6.31$  m), all trees with  $DBH \geq 11$  cm are recorded. And in the biggest area ( $r = 12.62$  m), all trees with  $DBH \geq 30$  cm are recorded. Each tree is assigned a group of trees of uniform tree species, stratum and diameter class. For each group, one individual tree with an intact crown is used to measure tree height representative of all trees of the same group. The stratum of each tree is recorded as one of three levels, encompassing the top layer (tree height is at least  $2/3$  of the stand's top layer), the second layer (tree height is lower than  $2/3$  of the stand's top layer but  $> 5$  m), and regeneration layer (trees with height  $\leq 5$  m). Individual retained trees that stick out of an otherwise significantly younger stand as part of a shelterwood cutting scheme are classified as such. Additionally, the slope of each inventory site is measured.

#### *Selection criteria*

To allow a systematic selection process, the research plots for this study were drawn from the pool of existing forest inventory sites. Using data from the 4,493 inventory sites surveyed in the Steigerwald region in the 2010 forest inventory, the tree species composition of the canopy layer was determined for each circular inventory site. The inventory sites were then filtered by the tree species composition of the top layer, selecting only sites containing one of the four target compositions of pure beech and beech-oak, beech-pine, and beech-spruce mixtures. These candidate sites were intersected with an additional, more coarse-grained dataset of the local forest company specifying the three leading tree species and the stand developmental stage of each management unit based on expert assessments after on-site inspections. Candidate sites in mature stands and with congruent tree species compositions on inventory sites and the management unit level were selected for the next step of the protocol. Of these remaining sites, those with slopes  $> 10\%$  were excluded from the pool.

In a next step, additional information on the remaining candidate sites was gathered using satellite imagery with 80 cm resolution (Digitales Orthophoto DOP80 WMS, Bayerische Vermessungsverwaltung) and the geographic information system ArcMap (ESRI ArcMap 10.5) and using the research plot dimensions of a 60 m x 60 m area around the center coordinate of the forest inventory sites. Sites were excluded if they showed a canopy cover of recognizably  $< 50\%$ , or if the distances from plot centers were  $< 100$  m for forest edges or  $< 30$  m for forest roads. The remaining 276 candidate sites that conformed with minimum distances and canopy cover were examined on site. For this, the corners of the 60 m x 60 m

plots were marked, and the share of basal area was estimated for each tree species present on the plot area. Additionally, the cover of the regeneration layer (tree height  $\leq 5$  m) and the stand age were estimated. With this information on the remaining 276 candidate sites, research plots were chosen based on the following criteria: For each of the mixed forest types, the share in basal area of the admixed species was 10–90 %. Non-target tree species in all forest types were present only up to a 10 % share in basal area of the top layer. Broadleaved stands had a minimum age of 80 years, and admixed conifers had a minimum age of 35 years. The maximum cover of the regeneration layer was 80 % and sites with standing or flowing bodies of water were dismissed. Out of the pool of candidate sites that conformed with the above criteria, research plots were chosen guaranteeing a minimum distance between plot centers of 200 m (100 m in strict forest reserves), an even distribution of basal area shares of admixed tree species along the admixture gradient, and an even distribution of research plots over the study region.



**Figure 1:** Map of the study region in northern Bavaria and location of research plots of 1 ha in managed stands and strict forest reserves (SFR).

### *Selected research plots*

A total of 61 research plots were selected for this study. Plots measured 60 m x 60 m, with the square area aligned along the north-south and east-west axes and the permanently marked



forest inventory coordinate at the plot center. The 41 research plots in managed stands included 9 beech-dominated plots, 11 mixed beech-oak plots, 10 beech-pine plots and 11 beech-spruce plots (Fig. 1). The share of basal area for the admixed tree species ranged from 11 to 77 % in beech-oak stands, from 11 to 42 % in beech-pine stands, and from 14 to 69 % in beech-spruce stands. 10 research plots each were chosen for beech-dominated stands and beech-oak mixtures in strict forest reserves, respectively (Fig. 1). Oak admixture in unmanaged beech-oak plots ranged from 21 to 71 % of the basal area. In the strict forest reserves, the minimum theoretical span since the last harvesting operation ranged between 7 and 19 years for most research plots but was likely higher throughout. At least one plot in the reserve "Kleinengelein" had not been managed for around 100 years. All research plots were marked at the plot corners and exempt from harvesting operations for the duration of the study.

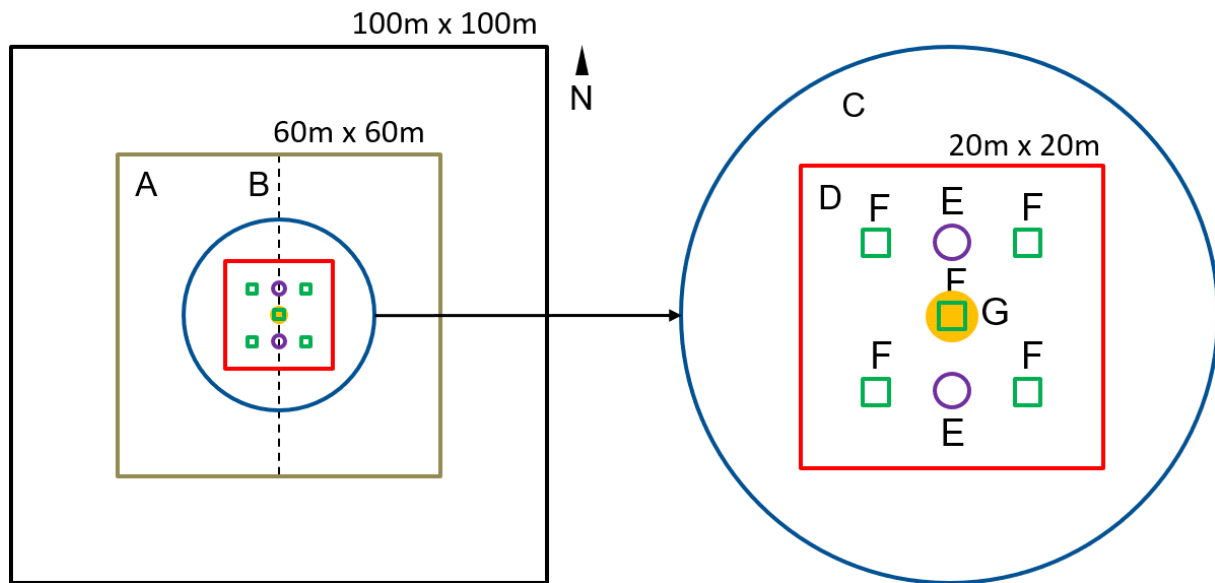
### 2.2.3. Inventory of forest structures

#### *Living stand inventory*

A detailed inventory of the living stand was carried out on all 60 m x 60 m plots between December 2017 and April 2018 by Sebastian Kienlein (Fig. 2A). For this, the diameter at breast height and the species of all trees with a DBH  $\geq 7$  cm were recorded. Additionally, the azimuth and the distance to the plot center were recorded, allowing a precise location of each tree.

#### *Deadwood inventory*

Following the guidelines of the forest inventories by the Bavarian state forest company, a detailed deadwood inventory was conducted on the 60 m x 60 m plots between December 2017 and April 2018 by Sebastian Kienlein (Fig. 2A). The diameter and length of any standing and lying deadwood object with a diameter  $\geq 20$  cm and a minimum height or length of 1.3 m were recorded to allow estimates of deadwood volume. The diameter of lying deadwood was measured 1.3 m from the thicker end. Analogously, the diameter of standing deadwood was measured as DBH. Whenever possible, the tree species was recorded. If not possible, the object was classified as either broadleaved or coniferous wood, or as non-determinable. Tree stumps from harvesting operations fell below the height threshold and were not considered for deadwood estimates.



**Figure 2:** Sampling design on each of the 61 research plots. Living stand and deadwood inventories and light measurements were conducted on (A) 60 m x 60 m. (B) Birds were surveyed on 100 m x 100 m using point-stop transect sampling on a 60 m line between the northern and southern edges of the 60 m x 60 m area. (C) Fungi were surveyed on a circular area of 1,000 m<sup>2</sup> around the plot center. (D) Plant surveys were conducted on 20 m x 20 m subplot. (E) Insects were sampled using two flight interception traps at 1.5 m above ground. (F) Litter sampling for soil arthropod extraction took place at 5 15 cm x 15 cm subplots. (G) Batcorders for the acoustic survey of bats were located at the plot center.

#### *Tree-related microhabitats*

Simultaneously with the living stand and deadwood inventories, tree-related microhabitats were recorded on each research plot by Sebastian Kienlein and Malte Graner. Structures visible from the ground were recorded on standing trees using binoculars. The mapping of structures was carried out along a spiral-shaped transect in a time-standardized way, starting at the plot center and lasting 60 minutes per plot. Classification of tree-related microhabitat structures followed the catalog created by Kraus et al. (2016). The habitat structure classes specified in Kraus et al. (2016) were then aggregated into the four categories "tree cavities", "crown deadwood", "bark structures" and "fungi and epiphytes". All structures were subsequently aggregated by category and plot over all individual trees.

#### *Light availability*

Between August and September 2017, light availability was measured on the 60 m x 60 m area of each research plot by Sebastian Kienlein (Fig. 2A). For this, a 5 x 5 rectangular grid with points spaced by 15 m was fit unto the plot, covering the entire plot area. At each of the 25 grid points, an automated fisheye lens camera (Solariscope SOL300, Behling) was used to measure the indirect site factor (ISF). The ISF measures the amount of indirect sunlight

as a percentage of the amount of light at a completely unshaded location (Annighöfer et al., 2019). All 25 light measurements per plot were compiled into a mean ISF value.

#### 2.2.4. Biodiversity surveys

I was responsible for the sampling designs for fungi, soil and litter arthropods, beetles and true bugs, birds and bats. I was also actively involved in the sampling of soil and litter arthropods, beetles, true bugs and bats, with the support of student helpers and technical staff. I furthermore supervised and participated in the processing of arthropod samples and bat calls. With the exception of bats, species-level identification was carried out by expert taxonomists. Details of the sampling methods are provided below.

##### *Plants*

Plants were surveyed twice on a 20 m x 20 m subplot around the plot center of each plot in May and June of 2017 (Fig. 2D) by Johanna Kózak. All vascular plant species were identified and their cover was estimated as a percentage of the plot area. Each observation was classified into one of four layers that included the herb layer, the shrub layer, and tree layers one and two.

##### *Fungi*

Three separate surveys of fungal fruitbodies were conducted on all plots by expert taxonomists (Markus Blaschke, Andreas Gminder, Michael Karasch). Surveys took place in April, September and November 2017 on circular subplots of 1,000 m<sup>2</sup> around the plot center (Fig. 2C). Subplots were searched for fungal fruitbodies of macromycetes with fruitbody diameters > 2 mm in a time-standardized way. 30 minutes were dedicated to the search for deadwood-inhabiting fungi on standing and lying deadwood. 15 minutes were dedicated to soil saprotrophs and mycorrhiza on the ground. Species were determined on-site if possible. If this was not the case, samples were taken for microscopic analysis. After identification, fungi were classified (by Markus Blaschke) into wood-decomposing species and fungi of other guilds, the latter including litter decomposers, mycorrhiza and fungal parasites.

##### *Soil and litter arthropods*

On five 15 cm x 15 cm subplots at the plot center and the corners of a 5 m x 5 m square around the plot center (Fig. 2F), litter samples were taken in October 2017. At each subplot, loose leaf litter and 1 cm of the upper organic layer (O<sub>H</sub> horizon) were collected and placed in air-tight plastic bags. Samples were then placed for 48 hours in a modified Kempson heat extractor (Kempson et al., 1963) to extract soil and litter dwelling arthropods. The extractor

successively increased the sample temperature from room temperature to 50 °C in steps of 5 °C per hour. Samples were weighed prior to and after extraction as the collected volumes differed depending on the magnitude of the litter and the upper organic layer. After extraction, samples were transferred to 70 % ethanol. Adult oribatid mites were determined to species, genus, or family level by Katja Wehner following Weigmann (2006). Collembola were determined to species level by Jörg Salamon.

#### *Beetles and true bugs*

Two flight interception traps were installed on each plot in late March 2017 for the sampling of beetles (Coleoptera) and true bugs (Hemiptera: Heteroptera). Traps consisted of a crossed pair of transparent plastic boards measuring 40 cm x 60 cm, with funnels leading to sampling jars at the bottom and the top (Gossner and Ammer, 2006). These sampling jars contained a 3 % CuSO<sub>4</sub> solution with a drop of detergent to reduce surface tension. Traps were installed 1.5 m above the ground 5 m north and south of the plot center (Fig. 2E). Traps were moved to the closest possible location in cases where regeneration layer vegetation impeded installation at the intended location. Sampling jars were emptied monthly until late September 2017 and catches were transferred to 70 % ethanol and identified to species level by Boris Büche. Beetles were additionally classified into saproxylic, i.e. deadwood-dependent species, and non-saproxylic species following Schmidl and Bussler (2004).

#### *Birds*

Birds were surveyed on each research plot using point-stop transect sampling (Moning and Müller, 2009). The 60 m north-to-south transect through the plot center ranged from the northern to the southern research plot boundary (Fig. 2B). Birds were identified by Matthias Bull based on sightings and calls along the transect. Surveys lasted for 1 minute at each the start and end points and 5 minutes at the plot center, in addition to the duration of the walk along the transect line between these three stops. Only individuals within a 100 m x 100 m area surrounding the plot center were recorded, and flyovers were disregarded. Each research plot was surveyed five times between late March and early June 2017. Mapping took place between sunrise and midday and no surveys were carried out in cases of rain or strong winds.

#### *Bats*

Bats were surveyed by standardized acoustic recordings using Batcorder 3.1 (ecoObs GmbH, Nürnberg) with the following specifications: quality = 20; threshold = -36 dB; post-trigger = 800 ms; critical call frequency = 14 kHz. Recorders were set up at the top of 2.5 m poles

at the plot center or as close to the plot center as possible while maintaining a minimum distance of 3 m to the nearest vertical structure (Fig. 2G). Recordings started one hour before sunset and ended one hour after sunrise. Sampling was not conducted in cases of rain or strong winds. Each research plot was sampled for one night every month from early June to late September 2017, resulting in four temporal replicates per plot. Recorded sequences contained zero to multiple bat calls and were submitted to a two-step identification process. The first step was automated species identification using batIdent (Marckmann and Runkel, 2010), which assigns one or more species or species groups (operational taxonomic units; OTU) to each recording based on comparisons of automatically measured call attributes with reference values. Random samples of results of automated species identification confirmed a high accuracy of the algorithm for the identification of *Pipistrellus pipistrellus* and the OTU 'Mkm' that includes the two *Myotis* species *Myotis bechsteinii* and *Myotis daubentonii* and the *Myotis* group *Myotis brandtii/mystacinus*. In a second step of manual quality control, sequences containing OTUs other than the above mentioned were re-checked manually by comparing call attributes including call structure and start-, end- and peak frequencies to keys by Skiba (2009) and Hammer et al. (2009). In cases of a mismatch between the result of the automated species identification process and the manual control, results of the batIdent output were adapted accordingly. Automated identification and subsequent manual checking yielded a dataset with 15 taxa including 10 species-level OTUs (*P. pipistrellus*, *Pipistrellus nathusii*, *Pipistrellus pygmaeus*, *Myotis myotis*, *Myotis alcathoe*, *M. bechsteinii*, *M. daubentonii*, *Myotis nattereri*, *Barbastella barbastellus*, *Nyctalus noctula*) and 5 above-species-level OTUs (*M. brandtii/mystacinus* including *M. brandtii* and *M. mystacinus*; “Plecotus” including both *Plecotus auritus* and *Plecotus austriacus*; “small Nyctaloids” including *Eptesicus nilssonii*, *Eptesicus serotinus*, *Nyctalus leisleri* and *Vespertilio murinus*; “Mkm” including *M. bechsteinii*, *M. brandtii/mystacinus* and *M. daubentonii*; “Myotis” including all species of genus *Myotis*). Bat recordings were additionally used to compute a measure of bat activity, defined as the number of 1-minute-intervals in a given night that contained at least one recorded bat call (Müller et al., 2012). Stationary social calls as by *N. noctula* were excluded for the calculation of bat activity.

### 2.3. Statistical analyses

To answer the various research questions, I used existing data from the long-term Biodiversity Exploratories project from the years 2008 to 2010 and newly surveyed data from the Steigerwald region in 2017 in a series of analyses. The main methods will be

presented in the following section, while detailed descriptions of the data collection methods and statistical analyses can be found in the respective manuscripts (Appendices A–C). All statistical analyses were performed in R 3.3.1 (R Core Team, 2018).

### 2.3.1. Effects of forest management on herbivorous insects

To assess the effects of forest management on herbivorous insects, I analyzed how management intensity, stand developmental stage and the tree species composition impacted three different feeding guilds of herbivorous insects in two forest strata using various subsets of 126 research plots from three regions of the Biodiversity Exploratories.

To analyze the impact of forest management on the abundance and species richness of the three guilds, linear mixed effect models were calculated using the *lme* function of the 'nlme' package in R (Pinheiro et al., 2018). Due to the unbalanced distribution of management intensities, developmental stages and main tree species across the three study regions, three different models were calculated. The first model, aiming at analyzing the effects of SMI on herbivorous insects, used 80 research plots in timber-stage managed conifer forests, managed beech forests and unmanaged beech forests from all three study regions. Analogous models were calculated with a reduced dataset of 23 research plots from all three study regions for the years 2008, 2009 and 2010 to test the consistency of effects across years. The second model, aiming at analyzing the effects of stand developmental stage on herbivorous insects, used a subset of 53 research plots in managed age-class beech forests from the two regions Hainich and Schwäbische Alb, where all four different developmental stages occurred. The third model, aiming at analyzing the effects of the dominating tree species on herbivorous insects, used a subset of 32 research plots in managed, timber stage age-class forests in the Schorfheide-Chorin study region, the only one where age-class forestry is performed in four different forest types in terms of dominating tree species.

All models included variables of forest structure and plant community as covariates. To reduce the number of covariates and ensure their independence, a Principal Component Analysis (PCA) was conducted using the *prcomp* function to calculate a singular value decomposition of the centered data matrix. Three independent PCA analyses were conducted based on the data sets for each model. From the variables entered into the PCA, those that correlated strongest with the first three axes were selected as covariates in the regression models. Response variables for all models were either abundance or species richness of xylophagous, leaf-chewing, and sap-sucking herbivores. After the covariates, the models included the explanatory variables for management intensity as measured by the continuous

index of silvicultural management intensity (SMI), for developmental stages as a factor variable with four levels, or for the dominating tree species as a factor variable with four factor levels. Each model included an interaction term between the fixed effect and a variable representing the forest stratum the trap was located in (canopy or understory). For the models regarding management intensity and developmental stage, the sampling region was added to the interaction term as data from more than a single geographically distinct study region was used. All models also included a plot-level identifier as a random factor to account for the replication within plots. For models on the species richness of herbivorous insects, the logarithmized abundance was included as a covariate to account for the influence of the number of sampled individuals on species richness (Gotelli and Colwell, 2001). Minimum adequate models were calculated by using stepwise elimination of non-significant terms in order of least significance.

To analyze the effects of management intensity, stand developmental stage and identity of the dominating tree species on the community composition of herbivorous insects, non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance matrices and using the 'vegan' package (Oksanen et al., 2018) was conducted on each of the subsets described above. The nested structure of the data was considered by using the *strata* argument. The effects of the covariates used in the above-described models on species composition were tested using the function *adonis* in the 'vegan' package.

### 2.3.2. Effects of tree species admixture on multiple taxa

To further assess the impact of tree species composition on forest biodiversity, I analyzed the effects of admixture of individual tree species to otherwise beech-dominated stands on plants, fungi, arthropods, birds and bats. These analyses were based on the dataset gathered from 41 managed research plots of four different forest types in the Steigerwald region in 2017 and 2018.

To assess differences between forest types of different tree species compositions regarding the plot-level abundance and diversity of the surveyed species groups, generalized linear models were calculated. Forest type (with factor levels beech, beech-oak, beech-pine and beech-spruce) was used as a categorical predictor variable and abundance and two metrics of alpha diversity of different species groups were used as dependent variables in as many models. Measures of alpha diversity included the number of species for all surveyed species groups and diversity as the exponential Shannon diversity index (Jost, 2007; henceforth 'Shannon diversity') for all groups but fungi, which lacked an abundance measure.

Abundances were numbers of individuals for arthropods and birds but cover for plants and minute calls as a measure of activity for bats. For each species group, abundance, species richness and Shannon diversity were tested in separate models. An additional model was specified with an index of multidiversity as the dependent variable. This index is the average proportional species richness across all species groups, calculated with standardized species richness values for each group by scaling them to the highest observed species richness across all forest types (Allan et al., 2014). To test whether the proportion of an admixed tree species regarding the total basal area significantly affected the species richness of the surveyed species groups, recursive partitioning analysis was conducted using the *ctree* function in the 'party' package (Hothorn et al., 2006). This function creates binary splits of the admixture proportion variable for each admixture gradient of either oak, pine, or spruce, identifying the split that maximizes association with the species richness variable. Subsets of the 41 research plots were created for this purpose, each consisting of the 9 pure beech stands and the 10 to 11 plots of the mixed stand forest types.

To assess the extent to which structural differences might have driven differences in alpha diversity between forest types, the effects of stand structure on the plot-level diversity of the surveyed taxa were investigated. First, generalized linear models were used to estimate differences between forest types regarding variables of stand structure and tree-related microhabitats. Next, generalized linear regressions were calculated for each of the surveyed species groups with species richness as a dependent variable and the above-mentioned measures of stand structure and tree-related microhabitats as explanatory variables.

While the analyses so far examined research plot-level effects of tree species composition, I also analyzed the effects of tree species admixture on a higher spatial scale. For this, I calculated differences in gamma diversity between forest types, i.e. whether the landscape-level species richness and Shannon diversity over all 41 research plots differed between forest types. I calculated frequency-based rarefaction curves for each forest type using the 'iNext' package (Hsieh et al., 2016). This was done separately for each species group and significant differences between forest types were derived from overlapping confidence intervals for the diversity equivalent to 10 research plots (Schenker and Gentleman, 2001).

Possible effects of tree species admixture on the community composition of the surveyed species groups were analyzed by conducting correspondence analyses (CA) on presence-absence-data for each species group using the *cca* function in the 'vegan' package (Oksanen et al., 2018). Permutational multivariate analyses of variance (PERMANOVA) were then



used to test for significant shifts in species composition using the *adonis* function from the same package. To not only document significant changes in the communities but also identify specialist species that are significantly associated with a certain forest type or combination of forest types, I conducted an indicator species analysis using the function *multipatt* in the 'indicspecies' package (Cáceres and Legendre, 2009). Possible forest type combinations were predefined (Cáceres et al., 2010) and included each forest type individually and combinations of both broadleaved forest types (beech, beech-oak) and of both mixed forest types (beech-spruce, beech-pine).

### 2.3.3. Differences between managed stands and strict forest reserves

To investigate how small forest reserves with a history of management might differ from the surrounding managed stands under progressive integrative forest management regarding the biodiversity of several taxa, I used a subset of 40 research plots in managed and unmanaged beech and beech-oak stands of the Steigerwald region. Data was gathered on all plots in 2017 and 2018.

First, I calculated generalized linear models to estimate the effect of forest management as a binary factor variable with levels "managed" and "strict forest reserve" and a continuous variable of oak admixture (the share of oak in total basal area) as well as their interaction on plot-level abundance and diversity of plants, saproxylic and non-saproxylic fungi and beetles, true bugs, birds and bats. Abundance measures for plants and bats were replaced by cover and activity measures, respectively. Alpha diversity included species numbers for all groups and Shannon diversity for all groups but fungi. Additionally, generalized linear models with identical explanatory variables were conducted on variables of forest structure and tree-related microhabitats, including the number of tree species, stand basal area, total deadwood volume, light availability, and the number of bark structures, tree cavities, crown deadwood objects, and fungal fruitbodies and epiphytes on trees. Poisson error distributions were used for count data, and Gamma distributions were used for continuous dependent variables. The limited number and spatial extent of the strict forest reserves in the study area led to an unavoidable geographic clustering of research plots in reserves. To avoid introducing biases, I checked for spatial autocorrelation in the residuals for each of the computed models (Dormann et al., 2007; Legendre, 1993). I calculated Moran's I using an inverse Euclidean distance matrix between the centers of the research plots with the function *Moran.I* in the 'ape' package (Paradis and Schliep, 2018). In cases of significant spatial autocorrelation in the residuals, I used the Moran eigenvector filtering function *ME* in the

'spatialreg' package (Bivand et al., 2013) with a row-standardized inverse distance matrix and a stopping threshold of  $\alpha = 0.2$  to choose eigenvectors that best reduced autocorrelation in the residuals. These eigenvectors were then used to re-fit the models (Griffith and Peres-Neto, 2006), and were successful in reducing spatial autocorrelation.

To evaluate whether differences in alpha diversity between managed stands and strict forest reserves could be attributed to differences in stand structure or availability of tree-related microhabitats, I estimated the effect of these variables on the abundance and species richness of the different species groups. Simple generalized linear models with single predictors were used, including the above-specified variables of stand structure and tree-related microhabitats. Each of these variables was centered by subtracting the variable mean from each value and then scaled by dividing by their standard deviations. This allowed the comparison of effect sizes between predictors of the same dependent variable. As with the regression models on abundance and alpha diversity, model residuals were checked for spatial autocorrelation and models were refit using eigenvector filtering if necessary.

To analyze how managed stands and strict forests differed in community composition of the analyzed taxa, I conducted correspondence analyses (CA) with the function *cca* in the 'vegan' package (Oksanen et al., 2018). CA were conducted separately for each species group using presence-absence data. Permutational multivariate analyses of variance (PERMANOVA) were used to test for significant effects of forest management and oak admixture on the species composition using the *adonis* function. I further used the function *multipatt* in the 'indicspecies' package (Cáceres and Legendre, 2009) to conduct an indicator species analysis to identify species that were significantly associated with a certain management (managed or strict forest reserve), forest type (beech or beech-oak), or combination thereof. The predefined combinations included each management and forest type individually and each possible combination of both variables.

### **3. Chapter overview**

This thesis contains three chapters consisting of two published research articles and one submission-ready manuscript. In the following, a summary and a description of author contributions will be presented for each chapter. The complete chapters are attached in Appendices A–C.

## **Chapter 1: Effects of forest management on herbivorous insects in temperate Europe**

Jan Leidinger, Sebastian Seibold, Wolfgang W. Weisser, Markus Lange, Peter Schall, Manfred Türke and Martin M. Gossner

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### **Summary**

As an essential component of nutrient cycling, herbivory is a key ecosystem function in forest ecosystems. It shapes plant community composition by altering plant resource allocation and competitive interactions. Among insects, herbivorous feeding habits are widespread. Through their position in the food chain, herbivorous insects relay effects of environmental changes to both higher and lower trophic levels in the ecosystem. Communities of herbivores are influenced by several abiotic and biotic factors, the latter including both bottom-up forces such as host plant identity, quality, and defense mechanisms, and top-down forces such as pathogen, predator and parasitoid pressure. Tree species composition, forest microclimate and other factors that potentially determine the abundance and species composition of herbivorous insect communities are strongly conditioned by anthropogenic forest management. In this chapter, I investigated how various aspects of forest management affect the abundance and species richness as well as the community composition of three different guilds of herbivorous insects in temperate European forests. Guilds included chewers and suckers of living plant tissue and xylophagous insects feeding on dead wood. Due to their different ecological niches, these guilds may be affected differently by forest management.

I analyzed data from 126 forests in three regions in Germany gathered by the Biodiversity Exploratories in 2008–2010. The forests included unmanaged and managed stands, and the latter included stands of different tree species composition, either dominated by beech, spruce, pine, oak, or mixed stands of beech and pine. Managed beech stands were further divided into developmental stages ranging from thickets to timber stage stands. The dataset included three feeding guilds (xylophages, leaf chewers and plant suckers) of herbivorous Coleoptera and Hemiptera from two different forest strata (understory and canopy). Forest management was characterized by its intensity as measured by the silvicultural management intensity index (SMI), by the stand developmental stage, and by the dominating tree species. Effects of forest management on insect herbivores showed consistent directions across regions, but responses of abundance and species richness varied between feeding guilds and

forest strata. While the abundance of herbivores tended to be negatively affected by forest management intensity (SMI) in the canopy layer, they increased in the understory. This result confirms that niche differentiation leads to distinct communities in the canopy and the understory and that they respond differently to management interventions. Regarding species richness, only plant suckers responded significantly to SMI, with slightly higher species richness at high management intensities. Positive effects of stand developmental stage on plant suckers and of all feeding guilds to stand biomass suggest a general positive effect of stand age on herbivorous insects. I further showed that oak forests harbor significantly higher species richness of leaf chewers and the highest abundance of plant suckers compared to beech, pine, and mixed beech-pine stands. Similarly, the canopies of pine and pine-beech forests showed a significantly higher species richness of plant suckers compared to pure beech stands. These findings confirm the importance of *Quercus* and *Pinus* as two of the most species-rich tree genera in Germany regarding Coleoptera and Heteroptera. Furthermore, all analyzed aspects of forest management significantly influenced the community composition of herbivorous insects.

Forest management strongly influences abundance, species richness and community composition of herbivorous insects. Its effects are mediated through management intensity but also through the favored tree species composition and the stand developmental stage, including effects of stand age and canopy openness. It remains important to note that canopies and the understory host different communities with individual responses to management, indicating that studies estimating the consequences of management interventions in forest ecosystems need to consider both forest strata. See Appendix A for the complete manuscript.

#### Author contributions

JL conducted the analysis and the writing of the original draft with the help of MG and SS. JL also prepared all figures. Study sites were selected by the Biodiversity Exploratories and data collection was supervised by MG, ML, MT, PS and WW. Conceptualization, data preparation and initial analyses were conducted by MG. All authors contributed to writing by reviewing and editing and approved the final manuscript.

## **Chapter 2: Admixing tree species affects biodiversity of multiple taxa in Central European beech forests**

Jan Leidinger, Martin M. Gossner, Sebastian Kienlein, Markus Blaschke, Kirsten Jung, Katja Wehner, Johanna Kozak, Anton Fischer, Reinhard Mosandl, Barbara Michler, Michael Ehrhardt, Anna Zech, Dennis Saler, Malte Graner, Sebastian Seibold, Wolfgang W. Weisser

Manuscript prepared for submission

### **Summary**

Focus on timber production as the primary objective of forestry operations has led to a dominance of economically profitable tree species, often grown outside of their natural range, in Central European temperate forest ecosystems. Due to properties like fast growth rates and versatile uses after harvesting, tree species like Scots pine, Norway spruce and oak have long management traditions in European forestry and today dominate managed forests, replacing naturally dominant tree species, usually European beech. Evidence of vulnerability to abiotic and biotic disturbances of these managed forests and efforts for the conservation of natural forest communities have led to changes in forestry policies, promoting a tree species composition with a higher proportion of broadleaved tree species that more closely resembles the local potential natural vegetation. These integrative management approaches seeking to balance resource production for human use with increased ecosystem stability and biological conservation will continue to rely on mixtures of tree species that include economically relevant species to realize their multiple objectives. In this chapter, I studied individual tree species admixtures of spruce, pine and oak to mature, naturally beech-dominated forest landscapes and its effects on the diversity and the community composition of several species groups.

Using data from 41 mature forest plots on herbaceous plants, wood-decomposing fungi and other fungal guilds, oribatid mites, springtails, true bugs, saproxylic and non-saproxylic beetles, birds and bats, as well as an index of multidiversity, I assessed the effect of tree species admixture on the abundance, species richness and diversity of these species groups. I compared pure beech stands with stands containing proportions of admixed tree species ranging from 11 to 77 % of the total basal area. I also analyzed the influence of variables of stand structure and tree-related microhabitats on the surveyed taxa. Furthermore, I analyzed differences in species richness between forest types on the landscape scale as well as differences in community composition and the existence of indicator species that are associated with a certain tree species mixture.

Results showed that the admixture of tree species to beech stands had only minor effects on the plot-level abundance and diversity of the surveyed taxa, with the majority of groups, including the index of multidiversity, showing no significant response. Analyses of variables of stand structure and tree-related microhabitats showed that admixtures led to significant differences in light availability and the number of crown deadwood objects. The strongest effects of admixture were found regarding landscape-level species richness, where higher species richness in one or several forest types with admixed tree species compared to pure beech stands was found for non-saproxyllic fungi, both beetle guilds, true bugs and herbaceous plants. The admixture of tree species also significantly altered community composition of six out of ten analyzed species groups, with every forest type, including pure beech stands, hosting specialist species significantly associated with that particular tree species combination.

This chapter shows that the admixture of tree species to beech forests affects local and landscape-level biodiversity by a combination of increased habitat heterogeneity and tree species-specific associations. The significant shifts in community composition and the presence of species with occurrences restricted to pure beech stands indicate that some portions of characteristic beech forest communities cannot be preserved in mixed forests. By benefiting specialist species that require structures or resources offered by the admixed tree species, admixtures can lead to higher landscape-scale diversity, but effects are highly species-specific both regarding the target taxon and the admixed tree species. See Appendix B for the complete manuscript.

#### Author contributions

JL participated in the conceptualization of the study and in defining the methodology of data collection together with JK, SK, AF, RM, MGo, SS and WW. JL carried out study site selection together with JK and Thomas Schäff. JL was in charge of arthropod sampling and supervising the sorting of trap catches by student helpers with the help of Kathrin Ziegler and Petra Freynhagen. Furthermore, JL was in charge of planning the acoustic survey of bats as well as creating a protocol for the manual identification of bat recordings together with KJ. AZ, DS and ME contributed to bat data collection and manual identification. JL was responsible for the collection of litter samples and assisted KW in the extraction of soil arthropods. JL was also responsible for data preparation, the formal analysis and the writing of the original draft including all figures.

Arthropod catches were identified to species level by hired taxonomists. Fungi were identified on-site and in the laboratory by MB and hired taxonomists. Bird surveys were carried out by an experienced ornithologist. Oribatid mites were identified to species level by KW and springtails by a hired taxonomist. Herbaceous plants were surveyed by JK. Living stand inventories and surveys of deadwood and light availability were carried out by SK. MGr carried out the survey of tree-related microhabitats under the supervision of SK. All authors contributed to writing by reviewing and editing and approved the final manuscript.



### **Chapter 3: Formerly managed forest reserves complement integrative management for biodiversity conservation in temperate European forests**

Jan Leidinger, Wolfgang W. Weisser, Sebastian Kienlein, Markus Blaschke, Kirsten Jung, Johanna Kozak, Anton Fischer, Reinhard Mosandl, Barbara Michler, Michael Ehrhardt, Anna Zech, Dennis Saler, Malte Graner, Sebastian Seibold

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#### Summary

In Central Europe, the predominant strategy for biodiversity conservation in forests is an integrative approach to forest management that seeks to reconcile the extraction of resources for human use with goals of biodiversity conservation within the same forest area. Integrative management often includes selective harvesting, uneven age structures, natural rejuvenation, retention of habitat trees and deadwood as well as segregative elements that exclude human intervention on a small scale. The benefits of management cessation and the resulting forest structures to biodiversity conservation, when compared to traditionally managed forests, are widely recognized. In this chapter, I investigated the contribution of small forest reserves with a history of management to biodiversity conservation in forest landscapes under integrative management.

I compared the biodiversity of plants, saproxylic and non-saproxylic fungi and beetles, true bugs, birds and bats between formerly managed forest reserves and stands under progressive integrative management. All research sites were located in forests dominated by beech and mixed forests of beech and oak, two typical forest types of Central European lowlands. I measured abundance, species richness and diversity of the surveyed taxa and recorded variables of forest structure to analyze whether structural differences drive the potential differences in biodiversity.

Local diversity was higher in forest reserves for birds and bats and higher in managed stands for plants and beetles, while fungi did not differ significantly between both. Managed stands and forest reserves also differed regarding some variables of stand structure, with higher total basal area and abundance of tree cavities in reserves and higher light availability in managed stands. These features explained some of the differences in diversity, with higher plant cover and species richness being a consequence of higher light availability and a contributing factor to increased beetle abundance and species richness in managed stands. Higher abundance of birds and bats in forest reserves, on the other hand, were likely associated with a higher average tree age and the presence of tree-related microhabitats.

The results show that recently established strict forest reserves with a long management history differ from forests under progressive integrative management in stand structure and microhabitat availability and consequently host partly different communities. Despite these differences, reserves preserved structural characteristics of managed forests and mostly comprised stands in the optimum stages of development, characterized by high basal area and low light availability before small-scale disturbances and natural senescence will set in at later stages. To benefit light and deadwood demanding species, new reserves should include early or late-successional stands. Oak admixture played no role in mediating plot-level differences between managed stands and reserves but was a significant driver of community composition and had a positive effect on the species richness of non-saproxyllic beetles, confirming the importance of the genus *Quercus* for the conservation of forest biodiversity. See Appendix C for the complete manuscript.

#### Author contributions

JL participated in the conceptualization of the study and in defining the methodology of data collection together with JK, SK, AF, RM, SS and WW. JL carried out study site selection together with JK and Thomas Schäff. JL was in charge of arthropod trapping and supervising the sorting of trap catches by student helpers with the help of Kathrin Ziegler and Petra Freynhagen. Furthermore, JL was in charge of planning the acoustic survey of bats as well as creating a protocol for the manual identification of bat recordings together with KJ. AZ, DS and ME contributed to bat data collection and manual identification. JL was responsible for data preparation, the formal analysis and the writing of the original draft including all figures with the help of SS.

Arthropod catches were identified to species level by hired taxonomists. Fungi were identified on-site and in the laboratory by MB and hired taxonomists. Bird surveys were carried out by an experienced ornithologist. Herbaceous plants were surveyed by JK. Living stand inventories and surveys of deadwood and light availability were carried out by SK. MGr carried out the survey of tree-related microhabitats under the supervision of SK. All authors contributed to writing by reviewing and editing and approved the final manuscript.

## **4. Discussion**

### **4.1. Main findings**

In three chapters, I investigated the effects of management intensity and particularly those of tree species composition and other forest structural attributes on the diversity of various taxonomic groups covering several trophic levels. The analyses included two large datasets. The first one, provided by the Biodiversity Exploratories, included data on 126 forest plots across three regions in Germany and 44,710 individuals of 698 species of herbivorous beetles, true bugs and cicadas. The second dataset was compiled with my active involvement and contained data on plants, fungi, springtails, oribatid mites, beetles, true bugs, birds and bats from 61 forest plots in the Steigerwald region.

In the first chapter, I showed that management intensity significantly altered communities of herbivorous insects. Management intensity affected the abundances of herbivorous insects in different ways, depending on the observed forest stratum. In the canopy, increasing management intensity tended to lead to a decrease in abundances, while responses in the understory were neutral to positive. In age-class beech forests, stand age was a driver of community composition of herbivorous insects. While the species richness of leaf-chewing insects was lowest in the canopies of timber-stage stands, the abundance of sap-sucking insects significantly increased with stand age. The tree species composition of the canopy layer also had a significant impact on the composition of all three feedings guilds of herbivorous insects, and oak stands exhibited a significantly higher species richness of leaf-chewing beetles and abundance of Hemiptera than all other stands. The canopies of pine and mixed beech-pine stands showed a significantly higher species richness of Hemiptera compared to pure beech stands.

In the second chapter, I showed that the admixture of tree species changed the species composition of six out of ten surveyed taxonomic groups. For each of the investigated forest types, there were specialist species significantly associated with that particular tree species combination. Local plot-level abundance, species richness and diversity differed between forest types of varying tree species admixtures only for few species groups. Gamma diversity, on the other hand, showed significant responses to tree species admixture for eight out of ten surveyed species groups, often with higher diversity in one or more mixed forest types compared to pure beech stands.

In the third chapter, I showed that strict forest reserves retain some structural characteristics of managed stands while differing in others. They also differed from managed forests in the community composition and alpha diversity of five out of seven analyzed taxonomic groups. The direction of the effects, however, differed between groups, with birds and bats benefiting from strict forest reserves and plants and beetles from managed forests. The described differences were consistent over forest types, but oak admixture again proved to be a significant driver of community composition.

#### **4.2. Effects of management intensity and contribution of strict forest reserves to conservation**

The results of chapters one and three confirm the widely accepted fact that forest management intensity has extensive consequences for forest biodiversity. But as previously shown by Paillet et al. (2010), the responses are heterogeneous between taxonomic groups, and even effects on single species groups varied significantly when observing different forest strata. I showed that abundances of all three feeding guilds of herbivorous insects were significantly affected by management intensity as measured by the silvicultural management intensity index (SMI). While the abundance of xylophages in the understory quadrupled from the lowest SMI values in unmanaged beech forests to the highest ones in intensively managed conifer stands, leaf-chewing beetles and sap-sucking true bugs and cicadas showed no significant response in that forest stratum. The positive response of xylophagous beetles to management intensity in the understory may be a consequence of more homogeneous habitats that result in less effective control by antagonists (Paine, 1980; Schmitz et al., 2000) and a function of resource availability. Saproxylic species are often more abundant in the understory (Gossner et al., 2013b), where amounts and diversity of deadwood are usually larger than in the canopy (Ammer et al., 2008), and beetle communities in the understory are known to differ from those in the canopy (Seibold et al., 2018). In the understory of

intensively managed stands, harvest remnants increase resource availability for saproxylic insects specializing on fresh deadwood. Effects in the canopy displayed the opposite pattern, with no responses at all or negative effects of SMI on herbivore abundances. The significant declines in numbers of leaf chewers and plant suckers confirm previous finding of negative effects of management intensity on canopy herbivores (Gossner et al., 2014a). In part, this decline might reflect feeding preferences of leaf chewers and plant suckers for broadleaved stands, as the management intensity spectrum usually reflects a gradient of increasing conifer admixture (Gossner et al., 2014b). Within tree functional groups, however, the reduction in herbivore abundances might reflect changes based on bottom-up or top-down forces along the management intensity gradient. Communities of herbivores in the understory and in the canopy differed significantly, and the contrasting reactions to management intensity might be a consequence of further functional differentiation even within feeding guilds. Similarly, the disproportionate effects of management interventions on the understory, where increased canopy openness leads to increased light availability and a higher cover and species richness of plants in the herb layer (Boch et al., 2013), might be responsible for the interaction of management intensity effects with forest stratum. Species richness of xylophages and leaf chewers did not respond to management intensity, and the number of sap-sucking insect species even increased with SMI. Thus, a more uniform stand structure and a lack of tree-related microhabitat diversity as features of management intensification (Bengtsson et al., 2000; Dieler et al., 2017), did not result in lower species richness of herbivores, even though communities were significantly altered. As with abundances, resource and habitat heterogeneity and tree species composition might be more effective drivers of species richness. Regarding both the effects of management intensity on abundance and species richness of herbivores, the relatively young age of the unmanaged stands included in the study might have in part masked the effects. Unmanaged stands had been abandoned for not more than 20–70 years at the time of the study (Schall et al., 2018b), and still preserved structural characteristics of managed stands.

Similarly, strict forest reserves in the Steigerwald project were mostly designated 7–39 years prior to sampling, which is representative for a large part of strict forest reserves in Central Europe (Meyer et al., 2011; Paillet et al., 2015). Classifying them into developmental stages revealed that the vast majority of research plots in reserves were in the mid and late optimum phases. While large-scale disturbances with very low canopy covers were excluded *a priori* due to a lack of potential replicates in reserves, this shows that even small-scale disturbances or senescence events are missing, confirming that Central European forests lack late-

successional stages (Hilmers et al., 2018; Paillet et al., 2015). The inventories of stand structure presented in chapter three showed that basal area was significantly higher and light availability in the understory was significantly lower in forest reserves compared to managed stands, in line with findings by Braunisch et al. (2019) who showed that this is a characteristic feature of recently established reserves in optimum-stage beech forests. The average deadwood volumes of  $19.3 \pm 0.5 \text{ m}^3 \text{ ha}^{-1}$  are comparable to the average value of  $23.8 \pm 4.2 \text{ m}^3 \text{ ha}^{-1}$  for European beech forests (Puletti et al., 2019) and recently established reserves (Christensen et al., 2005). Still, they are lower than values reported for old beech reserves (Christensen et al., 2005) and fall short of the range of 20–50  $\text{m}^3$  of deadwood per hectare deemed necessary for ecologically sustainable forestry by Müller and Bütler (2010). While higher deadwood volumes are usually expected in unmanaged forests (Seibold and Thorn, 2018), the surveyed forest reserves did not differ significantly from managed stands in deadwood volume. This lacking contrast in deadwood volumes may stem from the deadwood enrichment strategy in managed stands that has successfully increased deadwood availability in the study region (Doerfler et al., 2017) on one hand and from low natural tree mortality in the optimum-stage reserves on the other. A higher number of trees with cavities in forest reserves hints that stand structures in reserves and managed stands are starting to diverge, possibly due to a slightly higher average tree age in reserves and a delayed effect of the retention of habitat trees in managed stands that was only implemented in 2006. Confirming previous findings by Paillet et al. (2010), differences in abundances and alpha diversity between managed and unmanaged stands in the Steigerwald region were highly variable among species groups. While birds and bats were more abundant in forest reserves, higher abundances and species richness were found in managed stands for plants and beetles. Birds and bats are known to benefit from older stands (Moning and Müller, 2008) and have been found to react positively to management cessation before (Bouvet et al., 2016; Czeszczewik et al., 2015; Russo et al., 2010). Notably, results of the indicator species analysis revealed several indicator species for forest reserves that are known to rely on tree cavities, such as *Columba oenas*, *Ficedula albicollis* and *Myotis daubentonii* (Müller, 2005b; Winter and Möller, 2008). Another indicator species of forest reserves, *Phylloscopus sibilatrix* is sensitive to management-related structures and avoids internal edges, such as the ones created by forest roads (Bouvet et al., 2016). The analysis of effects of stand structure on abundance and species richness also showed that bats benefitted from higher mean basal area, likely an effect linked to higher tree age and higher availability of relevant microhabitat structures (Bütler et al., 2013). Cover and species number of plants, and abundances and

species numbers of saproxylic and non-saproxylic beetles were lower in forest reserves compared to managed stands. While increases in the cover and diversity of the herb layer have consistently been shown to be a quality of managed forests due to increased light availability (Abs et al., 1999; Boch et al., 2013; Paillet et al., 2010), previous studies are more ambiguous about the effect of management on beetles. The well-studied group of saproxylic beetles has been shown to react positively to management cessation (Müller et al., 2007b; Paillet et al., 2010), and especially species that indicate the presence of old-growth structures are more often found in forest reserves (Winter et al., 2005). Yet, abundances of saproxylic beetles can also benefit from increasing management intensity as shown in the first chapter of this thesis. This is most likely a function of habitat or resource availability, as stand structure can be a better predictor for the diversity of saproxylic beetles than management intensity (Bouget et al., 2014a). Indicator species for managed stands included the ambrosia beetle *Xyleborus saxeseni* and the invasive *Xyleborus germanus*, early colonizers of fresh beech deadwood and likely benefiting from harvest remnants in managed forests. The increased cover of the herbaceous layer itself might in part be responsible for increased abundance and diversity of saproxylic beetles in managed stands. Both fresh deadwood and the number of flowering plants drive the species richness of certain saproxylic beetles (Müller et al., 2008). As deadwood amounts in forest reserves increase due to natural mortality and disturbances and eventually exceed those in managed stands, abundances and alpha diversity of saproxylic insects are expected to increase. This will potentially also apply to saproxylic fungi, which did not exhibit significant differences in species richness in our study. Deadwood-inhabiting fungi did show a shift in species composition, indicating differences in functional composition that may be caused by differences in key attributes such as deadwood diameter or diversity of decay stages between reserves and managed stands (Bässler et al., 2014; Blaschke et al., 2009). This is supported by the fact that *Gloeoporus pannocinctus*, a specialist of large-diameter deadwood in old-growth stands (Blaschke et al., 2009) proved to be significantly associated with forest reserves.

Chapters one and three show that forest management intensity strongly influences forest communities, including taxa from various trophic levels. The species composition of most taxa changes along a gradient of management intensity, and abundance and diversity are often affected at the plot level as well. Species groups respond differently to management intensity, with some groups benefiting from very low management intensities while others are more abundant, more diverse, or both, in more intensively managed stands. The effect can even vary within taxonomic groups when comparing different habitat niches, such as the

canopy and the understory of the same forest stand. This hints at a strong influence of functional traits on the response to management, an assumption that is supported by the indicator species analysis that identified many old-growth specialists among the species significantly associated with forest reserves. Effects might be masked by the relatively young age of the unmanaged research plots throughout the studies, meaning that the potential contrasts between unmanaged stands and forests with intermediate or high management intensities might be stronger than the current state of unmanaged forests allows to infer.

Besides their pivotal function for research on natural forest processes, strict forest reserves are needed to allow natural selection to take place and, not least, provide habitat for species with low dispersal abilities that require long habitat traditions and for species that rely strictly on very old trees and high deadwood volumes and diversity (Gossner et al., 2013a; Lachat and Müller, 2018; Paillet et al., 2010; Walentowski et al., 2010). Even though the absence of anthropogenic disturbance alone can be a factor in determining the value of reserves for certain taxa (Coppes et al., 2017), differences between unmanaged and managed stands will mostly be caused by differences in forest structure, i.e. the availability of the above-mentioned old-growth features as habitats and resources and their quality and diversity. Today, the majority of forest reserves in Central Europe are derived from managed forests, where late-successional stages are notoriously lacking (Hilmers et al., 2018). Consequently, and as confirmed by our assessment of forest developmental stages, forest reserves are mostly still in the early to mid-optimum stages (Paillet et al., 2015). At the other end of the scale, continuous cover forestry and rapid afforestation after natural or anthropogenic disturbances have also led to a lack in the species-rich early successional developmental stages (Swanson et al., 2011). In chapter three, the biodiversity of forest reserves was compared to that in surrounding stands under a progressive integrative management approach and overall low management intensities. There was significant overlap between communities in forest reserves and managed stands for the surveyed species groups, confirming that a large portion of forest biodiversity can be supported in forests with an integrative management approach (Brunet et al., 2010; Schulze, 2018; Walentowski et al., 2010), especially when including deadwood enrichment strategies (Doerfler et al., 2018; Sandström et al., 2019). But the recently established reserves also showed first signs of developing structural attributes that set them apart from managed stands, leading to diverging community composition and abundances for the investigated species groups. Several red-listed indicator species were found for forest reserves, confirming that complete management cessation plays a crucial role in protecting susceptible species even in a



landscape of progressively managed forest and natural tree species compositions. The results also show once more that light availability and deadwood volume are important drivers of biodiversity. Given the generally low availability of both in recently established forest reserves, biodiversity conservation in forests would benefit from the inclusion of more structurally diverse sites, including early successional stages (Swanson et al., 2011), in the selection of future forest reserves. Active restoration measures emulating disturbances and structural characteristics of forests in late developmental stages should be considered (Sandström et al., 2019), especially in areas with strong legacies of management in the form of homogeneous age-class stands in early optimum phases or with a prevalence of non-native tree species.

### **4.3. Effects of tree species composition on forest biodiversity**

Throughout all chapters of this thesis, the tree species composition of the forest canopy layer was found to significantly affect forest biodiversity, with different forest types hosting distinct communities and differing in local and landscape-level diversity. In chapter one, I analyzed the effect of the leading tree species on three feeding guilds of herbivorous insects in a single study region of the Biodiversity Exploratories, finding that oak significantly increased the species richness of leaf-chewing beetles and the abundance and species richness of plant-sucking true bugs and cicadas. Also, leaf chewers were less abundant in pine canopies compared to beech stands, while more species of plant suckers were found in the canopies of pine and pine-beech stands compared to those of pure beech stands. Lower abundances of leaf-chewing beetles in pine canopies are most likely a consequence of their preference for broadleaved host species. The remaining effects emphasize the importance of oak and pine as drivers of forest biodiversity compared to other tree species. This is in line with findings by Brändle and Brandl (2001), who showed that *Quercus* and *Pinus* are among the most species-rich tree genera in Germany regarding Coleoptera and Heteroptera. With the exception of *Salix*, oak hosts the highest number of specialist species (Brändle and Brandl, 2001; Gossner, 2008). Somewhat surprisingly, mixed stands of pine and beech never exceeded both pure beech and pure pine stands regarding abundances and species richness of herbivores, even though previous studies have reported an increase in species richness of saproxylic beetles with the number of tree species (Gossner et al., 2016; Müller et al., 2015). This lack of tree species richness effects is in contrast with previous findings by Sobek et al. (2009) and might indicate that tree diversity effects on herbivores are highly variable depending on the species identity of both trees and herbivores (Vehviläinen et al., 2007).

The importance of oak was again confirmed by the dataset of the Steigerwald region presented in chapters two and three. Regardless of whether research plots were located in managed or unmanaged stands, the admixture of oak led to a significant increase in the abundance and species richness of non-saproxyllic beetles and the abundance of saproxyllic beetles, as well as to shifts in species composition for fungi, non-saproxyllic beetles and birds. Oak also stood out when analyzing the effects of single-species admixtures in managed beech forests. On the research plot level, mixed beech-oak stands had the highest abundance and species number of true bugs (albeit significantly differing only from beech-pine stands) and diversity of non-saproxyllic beetles (significantly differing only from beech-spruce stands). The results also showed that the proportion of admixture matters, with significantly higher beetle species richness in stands with an oak proportion of at least 28 % of the basal area. These differences were reflected at the landscape-level, where the diversity of true bugs was highest in beech-oak stands and the diversity of non-saproxyllic beetles was highest in beech-oak and beech-pine stands. These tree species preferences reflect the prominent role of genera *Quercus* and *Pinus* for the biodiversity of beetles and true bugs already discussed above (Brändle and Brandl, 2001; Walentowski et al., 2010), suggesting that these effects are largely tree species-specific. Other local alpha diversity effects in the Steigerwald dataset were scarce, with the exception of a high diversity of saproxyllic beetles and birds in beech-spruce stands. These were in part effects of light availability, which was lowest in pure beech stands and highest in mixtures with spruce, and the functional diversity of trees, especially relevant to birds (Ampoorter et al., 2019), and to saproxyllic insects by increasing the diversity of deadwood (Seibold and Thorn, 2018). Gossner et al. (2016) also found a higher diversity of saproxyllic beetles in spruce deadwood. The importance of functional diversity is underlined by the indicator species analysis, that identified bird species with a known association with coniferous trees like *Peripatus ater*, *Lophophanes cristatus* and *Regulus ignicapilla* (Müller, 2005b) to be indicators of coniferous admixture. It is the higher structural complexity of mixed stands (Juchheim et al., 2019) that ultimately drives species richness by affecting habitat heterogeneity (Heidrich et al., 2020; Stein et al., 2014).

The effects of increased structural heterogeneity are not restricted to the research plot scale, as effects of tree species admixture on species richness and diversity were more pronounced at the landscape level, i.e. regarding gamma diversity. In addition to the positive effects of oak on true bugs and oak and pine on non-saproxyllic beetles, there were higher diversities of oribatid mites and saproxyllic beetles in stands with admixed conifers, a higher diversity of non-saproxyllic fungi in beech-spruce stands, and a higher diversity of herb layer vascular

plants in all forest types with admixed tree species. Plant communities did not differ significantly between forest types, suggesting that the plant species added by the admixture of tree species were not tree species or mixture-specific but rather a product of increased light availability compared to the light-poor beech stands (Cavard et al., 2011). This was supported by a very low number of indicator species among plants. These were only *Carex pallescens* and *Brachypodium sylvaticum* for beech-spruce stands, two typical forest species (Honnay et al., 1998) that are light-demanding (Tinya and Ódor, 2016) and especially abundant on recently disturbed sites. It has been shown before that forest management and soil conditions are stronger drivers of the herb layer flora than the tree species of the canopy layer (Augusto et al., 2003; Barbier et al., 2008; Chamagne et al., 2016). Other differences in gamma diversity between forest types were also linked to resource and habitat availability: A high diversity of soil arthropods usually coexists at a small spatial scale (Wehner et al., 2016), with communities often shifting significantly among samples of the same litter type (Hansen and Coleman, 1998). Soil arthropods are known to be strongly shaped by bottom-up forces like abiotic factors and the soil microbial communities (Korboulewsky et al., 2016; Lange et al., 2011; Scheu et al., 2003), and the humus of coniferous stands supports higher abundances of oribatid mites (Maraun and Scheu, 2000), a possible explanation for their higher landscape-scale diversity in stands with admixed conifers. Eissfeller et al. (2013) have previously shown that oribatid mites benefit from recalcitrant persistent litter compared to rapidly decomposing material of high nutrient quality such as oak litter, explaining the low overall diversity of mites in oak stands. Equally an effect of habitat and resource availability, a higher diversity of saproxylic beetles in mixed broadleaved and coniferous stands reflects the increased light availability and functional tree diversity discussed above. A high affinity of saproxylic beetles for spruce has previously been shown by Müller et al. (2015) and by Gossner et al. (2016), a fact they attributed to a high share of conifer specialists and the overall high resource availability of spruce in Germany. Saprotrophic and mycorrhizal fungi also had a high gamma diversity in beech-spruce stands, an effect driven in part by the presence of spruce specialists like *Phragmotrichum chilletii* and *Mycena metata* as shown by the indicator species analysis. Ectomycorrhizal fungi have been found to be more diverse in mixed stands, attributed to the addition of fungi species associated with each tree species (Cavard et al., 2011), and the larger amount of non-target tree species in beech-spruce plots, and consequently sporadic occurrences of ectomycorrhizal fungi associated with these non-target tree species, might have contributed to higher gamma diversity.

Admixtures of tree species to beech significantly changed the community composition of most surveyed species groups. Only plants, springtails and bats did not experience significant shifts in community composition due to the admixture of tree species. Birds and saproxylic fungi, while not exhibiting any gamma diversity differences between forest types, still experienced significant shifts in community composition. This is in line with findings of strong host tree preferences by Purahong et al. (2018) for fungi and strong effects of functional tree species composition on birds (Ampoorter et al., 2019). Indicator species were most numerous for the broader categories of pure broadleaved and mixed broadleaved-coniferous stands, including species from all surveyed groups but plants. The marked difference in functional traits between angiosperms and gymnosperms usually causes equally marked splits in the communities of species with high host specialization, confirming once again the importance of functional tree diversity (Ampoorter et al., 2019; Brändle and Brandl, 2001). While the admixture of tree species often led to significant shifts in community composition and to the promotion of species associated with the admixed tree species or particular structures in mixed stands, it remains to be investigated to which degree the communities of pure beech stands constitute subsets of the communities in stands with admixed tree species. For each species group but plants, springtails, birds and bats, there were species significantly associated with pure beech stands (one bird species, *Columba oenas*, was identified as an indicator of pure beech stands in forest reserves in chapter one, but this is rather an effect of tree cavity availability than one of tree species identity). While beech forests host a relatively low amount of specialist species compared to other forest types (Walentowski et al., 2010), this shows that a portion of the biodiversity of beech forests might be displaced by the admixture of other tree species. In our dataset, this for example included the beetle *Triplax rufipes*, a species that relies on the presence of fungi of the genus *Pleurotus* such as *Pleurotus ostreatus*, known to have a high host preference for beech. Both species were significantly associated with pure beech stands in this study. Many indicator species were also found for broadleaved stands in general, including beech and mixed beech-oak stands, setting them apart from stands with less natural tree species compositions due to coniferous admixtures.

With the above results, I showed that forest management decisions concerning the tree species composition will, even for forests under a homogeneous management regime and reducing confounding factors such as forest age and canopy cover, have wide-ranging effects on species groups of all trophic levels from belowground to highly mobile aboveground taxa. This confirms the key role that this trophic level plays in the shaping of forest communities

from the bottom up (Price, 2002). The findings on the effects of tree species admixture on forest biodiversity, however, are limited by our selection of methods and investigated species groups. Arthropods were only sampled in the understory, but the strong vertical stratification of forest communities (Floren et al., 2014; Gruppe et al., 2008; Ulyshen, 2011) and diverging responses to management as shown in chapter one suggest that groups like canopy arthropods might show a different, or stronger, response to tree species composition. Similarly, the use of entire species groups as study subjects suggests a homogeneity in responses to environmental factors that neglects large within-group variability (Bouvet et al., 2016; Renner et al., 2018). For effective biodiversity conservation, a more detailed understanding of functional groups and individual species and their relationships with forest management and structure will be needed.

Pure beech forests in Central Europe are relatively young – in geological and evolutionary terms – and there is only a limited number of beech specialists, while a large part of the associated biodiversity is made up of generalists often shared with *Quercus spp.* and other broadleaved species (Walentowski et al., 2010). My results show that oak, a tree species with frequent co-occurrence with beech in Central European forests, has the potential to significantly boost forest biodiversity if admixed to beech. Oak is even indispensable for the conservation of certain species groups such as true bugs (Sobek et al., 2009). The results also show that the increased light availability necessary for the regeneration of oaks (Mölder et al., 2019) will have additional positive effects on forest biodiversity. Further research should explore the potential of other, less common tree species that are natural parts of many beech forest types, like tree genera *Tilia* and *Carpinus*, to enhance biodiversity in beech forests. Spruce and pine, while also native to Central Europe, are mostly artificially sustained in their current range. Nonetheless, the admixture of these species was not detrimental to plot-level diversity and even increased alpha and gamma diversity for a number of taxa. Yet, natural beech forests contain unique communities that can host large shares of many species groups over a gradient of different developmental stages (Müller et al., 2013). The special responsibility of Central Europe for this forest type (Knapp et al., 2007) demands the preservation of stands with natural tree species compositions at a larger scale than guaranteed by the network of forest reserves and national parks. Thus, the availability of different mixtures and pure stands at the landscape scale might be necessary for effective biodiversity conservation in forests (Heinrichs et al., 2019), confirming that no single management regime can effectively reconcile all required functions (Felipe-Lucia et al., 2018).

#### 4.4. The role of forest structure

Forest management intensity and tree species composition exert a strong influence on the community composition, abundance and diversity of many forest taxa. While some effects may be attributed in part directly to the presence or absence of humans and related disturbances (Coppes et al., 2017) and to evolutionary ties to certain tree species (Sprick and Floren, 2008), most biodiversity effects of both management intensity and tree species composition are translated via a variety of stand features (Gossner et al., 2014b). The strong ties of forest communities to specific habitats within forest stands are reflected in the strong vertical stratification of forest communities (Floren et al., 2014; Gruppe et al., 2008; Ulyshen, 2011) that led to significantly different insect communities in the understory and canopy layers as described in chapter one. These differences are a consequence of variations in habitat and resource quality and availability, such as higher availability and diversity of deadwood in the understory (Seibold and Thorn, 2018) or the preference of many Heteroptera species for the sun-exposed upper canopy (Gossner, 2009).

In chapter one, I showed the importance of stand structure for forest biodiversity by analyzing the effects of forest age along a gradient of forest developmental stages. In traditional age-class forestry systems, stands consist of individuals of a single age cohort, leading to structurally homogeneous stands (Puettmann et al., 2012). As stands age, they undergo a series of deep structural changes, developing from thickets to more mature pole-wood stages and later reaching mature timber stages, while terminal and decay stages of forest development are usually not present in managed forests (Hilmers et al., 2018). Along this gradient of stand age, various structural parameters like tree density, total basal area, light availability and the abundance of tree-related microhabitats vary considerably. The results show that at the same time, communities of all investigated feeding guilds of herbivorous insects significantly shift their species composition. Stand biomass was a significant driver of community composition for all feeding guilds and has been shown to be a suitable proxy for stand age, with saturation reached at age 120–140 due to harvesting (Schall et al., 2018a). Considering that common harvesting cycles in managed age-class stands allow a maximum stand age of 80–120 years while animal and plant diversity significantly increase in the later forest developmental stages (Hilmers et al., 2018), these results might have underestimated the effects of stand age on forest herbivores. Stands supported an increasing number of Hemiptera individuals as they aged, with similar but non-significant trends in both other guilds but overall positive effects of stand biomass. Older

stands, especially multi-layered ones, offer a larger amount of resources in the form of leaves, and these effects are likely the product of increasing resource availability. Nonetheless, it is difficult to disentangle the effects of increasing resource availability from effects of increasing habitat and resource heterogeneity (Müller et al., 2018). Considering evidence for increased species richness and density of herbivores with forest age (Jeffries et al., 2006), these results suggest positive effects of longer rotation periods for the biodiversity of age-class forests.

Forest structure also played an important role in mediating the effects of management intensity on the community composition and diversity of several taxonomic groups for stands of comparable age and developmental stage. As discussed in chapter one, tree density, plant species and stand biomass were significant drivers of the community composition of herbivorous insects along a gradient of management intensity. The positive response of the abundance of herbivores to increasing SMI as discussed above might have been a consequence of greater structural homogeneity in intensively managed stands resulting in less effective control by antagonists (Paine, 1980; Schmitz et al., 2000). Variables of stand structure were also able to partly explain the differences in local abundances and biodiversity between managed and unmanaged beech and beech-oak stands in the Steigerwald region. For instance, basal area and tree cavities both significantly increased bat activity, indicating that they were the driving force behind higher bat activity in forest reserves (Paillet et al., 2018). Similarly, light availability and basal area were significant predictors of plant cover and beetle species richness, and responsible for their preference for managed stands. Positive effects of light availability on birds (Moning and Müller, 2008), a group that was significantly more abundant in the on average older and darker stands in forest reserves, show that no single structural feature or management category should be used to predict effects of stand structure on biodiversity. Schall et al. (2018a) have previously shown this, emphasizing the necessity to use multiple structural features to describe stand structure and analyze possible effects on biodiversity. Other effects of structural features on biodiversity, such as positive effects of deadwood on the species richness of fungi, did not reflect effects of management intensity, confirming that structural features might be able to capture additional variation in the data compared to mere categories of forest management (Gossner et al., 2014b). Finally, two prominent structural attributes that have often been described as key drivers of forest biodiversity also yielded consistently positive effects in this study: Deadwood availability benefitted fungal species richness, saproxylic beetles, birds and bats

while light availability had positive effects on plants, beetles and birds, confirming their importance for forest biodiversity in general.

#### **4.5. Future directions**

A multitude of studies has been dedicated to the effects of forest management on biodiversity in temperate Central European forests (Brunet et al., 2010; Paillet et al., 2010), but the diversity of forest types, management regimes, land-use histories and habitats and species potentially affected by these still holds many open questions. This study has shown that forest taxa respond to anthropogenic management in different ways depending on functional traits such as feeding guilds, or on the preferred habitat within a forest stand. Although much progress has been made in identifying key structures that relay effects of management interventions on biodiversity, for more effective conservation of forest taxa it will be necessary to examine relationships between species and structural attributes on even finer scales.

The value of old-growth attributes and primary forests for conservation has also been widely discussed. While this work contributes to the understanding of how strict forest reserves complement forests under integrative management in the conservation of biodiversity, it only constitutes a snapshot in an evolving landscape. How progressing forest development in reserves, including an increase in late – and early – successional stages (Paillet et al., 2015) and changing practices in managed stands will modify this balance should be the topic of future research.

This study also showed that admixture of tree species in beech forests significantly affects forest biodiversity by altering communities and leading to changes in alpha and gamma diversity. Large variation in alpha diversity and community composition within forest types with different proportions of admixed tree species and some effects of admixture proportion on biodiversity hint at strong dependencies of forest communities on the exact local tree species composition. Further analyses are required to establish the degree of nestedness of communities of pure beech stand and those of mixed stands, and whether communities of mixed forests include specialist species that rely on small-scale tree species mixtures rather than constituting only a combination of generalists and specialists of individual tree species (Cavard et al., 2011). Answers to this question will allow informed decisions on the conservation of natural Central European beech forests and their communities. Additionally, much can be learned from changing the spatial scale at which biodiversity effects of forest management, especially tree species composition, are investigated. On a finer scale, the



spatial arrangement of tree individuals of different species within stands might define habitat suitability for certain species (Müller and Gossner, 2007; Wehnert and Wagner, 2019), while at a larger spatial scale, the mixture of different forest types within a landscape can be optimized for conservation purposes if the individual communities are known (Heinrichs et al., 2019).

Finally, research on forest management and biodiversity needs to view its findings in the context of changing environmental conditions. Climate change will alter the disturbance regime (Seidl et al., 2011), the potential geographical ranges of tree species (Kölling et al., 2009; Schuldt et al., 2020), and will put species struggling with the impacts of anthropogenic land use under additional stress (Hof et al., 2011). Future research should take into account that climate change will impact forests and the communities they host (Hickler et al., 2014) if its goal is to support the effective conservation of biodiversity in the coming decades and centuries.

## 5. Conclusion

The analysis of two large datasets in Central European temperate forests allowed me to draw conclusions on a variety of forest management effects on forest biodiversity. It was shown that all investigated aspects of management – a gradient of management intensity, the establishment of strict forest reserves in forests under integrative management, and tree species composition – significantly impact many taxonomic groups. The magnitude and the direction of the effects vary between species groups, and within groups, they depend strongly on traits like the feeding guild and the preferred forest stratum.

The complete cessation of management in strict forest reserves contributes to the conservation of forest biodiversity by benefiting some taxa, mainly those reliant on old-growth structures that are limited to aged stands. Yet, unmanaged stands with a history of management retain structural attributes of managed stands, and biodiversity conservation would profit from including more structurally rich stands in terminal or decay stages, as well as early-successional stages after disturbances, in the designation of new reserves. Most effects of forest management are mediated by changes in forest structure that affect habitat and resource availability and diversity. In managed forests, increasing the amount and diversity of deadwood remains an effective way to preserve many taxonomic groups. Similarly, creating small-scale disturbances that increase light availability will not only benefit plants, but promote a number of other species groups including beetles and birds through cascading trophic effects and higher habitat heterogeneity. Increasing the length of rotation periods, combined with less dense canopies in mid and late developmental stages, will be beneficial for herbivorous insects and other taxa. Forest management should also place special emphasis on the composition of tree species. Tree species admixtures affect local and landscape-level biodiversity via a combination of changes in structural attributes and species-specific associations. In particular oak, and to a slightly lesser degree pine,

contribute to the conservation of forest biodiversity with an above-average amount of associated species. Mixing tree species with interspecific differences in physiological and morphological traits will increase the heterogeneity of stand features, increasing niche diversity with a larger number of available resources and habitats. These admixtures can increase local abundances and diversity of forest taxa, and a combination of stands of natural tree species composition and functionally diverse mixtures will benefit overall landscape-scale biodiversity. Forestry decisions to increase the share of mixed stands should consider that tree species admixture shifts community composition away from typical beech forest communities, and future research should focus on quantifying admixture thresholds and configurations of forest type and management intensity combinations at higher spatial scales that optimize biodiversity conservation.



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## **Appendix A: Chapter 1**

### **Effects of forest management on herbivorous insects in temperate Europe**

This article is available upon request (please contact [jan.leidinger@tum.de](mailto:jan.leidinger@tum.de)). It is also available at <https://doi.org/10.1016/j.foreco.2019.01.013>.

## **Appendix B: Chapter 2**

### **Admixing tree species affects biodiversity of multiple taxa in Central European beech forests**

This article is available upon request (please contact [jan.leidinger@tum.de](mailto:jan.leidinger@tum.de)).

## **Appendix C: Chapter 3**

### **Formerly managed forest reserves complement integrative management for biodiversity conservation in temperate European forests**

This article is available upon request (please contact [jan.leidinger@tum.de](mailto:jan.leidinger@tum.de)). It is also available at <https://doi.org/10.1016/j.biocon.2020.108437>.