DIVERSITY OF SAPROXYLIC BEETLES AND HOST TREE SPECIALISATION IN DIFFERENTLY MANAGED FORESTS ACROSS GERMANY

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„Befreien wir uns von allem, was wir zu wissen glauben und schaffen wir Platz für die Erkenntnis"

Jan Josef Liefers als Prof. Dr. Karl-Friedrich Boerne (Tatort, Folge 517 - Fakten, Fakten)

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EHRENWÖRTLICHE ERKLÄRUNG

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel *„Diversity of saproxylic beetles and host tree specialisation in differently managed forests across Germany“* selbstständig am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter der Anleitung und Betreuung durch Herrn Prof. Dr. Ingolf Steffan-Dewenter und Herrn Prof. em. Dr. Karl Eduard Linsenmair angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weitere akademische Grade erworben oder zu erwerben versucht.

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SUMMARY

Chapter I

The gradual turnover of dead organic material into mineral nutrients is a key ecological function, linking decomposition and primary production, the essential parts of the nutrient-energy cycle. However, disturbances in terms of species or resource losses might impair the equilibrium between production and decomposition. Humanity has converted large proportions of natural landscapes and intensified land-use activity for food production. Globally, only very few areas are totally unaffected by human activity today.

To ensure the maintenance of both essential ecosystem services, knowledge about the interplay of biodiversity and ecosystem functioning as well as effects of intensified management on both is crucial. The vast majority of terrestrial biomass production as well as decomposition take place in forest ecosystems. Though forestry has a long sustainable history in Europe, its intensification during the last century has caused severe impacts on forest features and, consequently, on the associated biota, especially deadwood dependent organisms. Among these, saproxylic beetles are the most diverse group in terms of species numbers and functional diversity, but also most endangered due to habitat loss. These features classify them as ideal research organisms to study effects of intensified forestry on ecosystem services. The BELONGDEAD project located in Germany aimed to investigate deadwood decay and functional consequences of diversity changes in the associated fauna on the decomposition process from the initialisation of deadwood decay to complete degradation.

As part of the BeLongDead project, this dissertation focussed on saproxylic beetle species, thereby evaluating (1) regionally effects of tree species identity of fresh deadwood and (2) forest management of varying intensities on the diversity, abundance and community composition of saproxylic beetles (chapter II); (3) the specialisation degree of different trophic guilds of saproxylic beetles, and thus the stability and robustness of their interaction networks against disturbances (chapter III); (4) the impact of environmental features of local to regional spatial scales on species richness of saproxylic beetles differing in their habitat niche in terms of deadwood decay stages (chapter IV).

Chapter II

The vast majority of European forest ecosystems have been anthropogenically affected, leaving less than 1% of the about 1 milliard hectare as natural forests. A long history of forestry and especially the technological progress during the last century have caused massive habitat fragmentation as well as substantial loss of essential resources in European forest ecosystems. Due to this, the substrate-dependent group of saproxylic beetles has experienced severe species losses. Thus, investigations concerning saproxylic diversity and deadwood volume were badly needed. However, the importance of different deadwood in terms of tree species identity for the colonization by saproxylic beetles under different local and regional management regimes is poorly understood. Therefore, we studied possible regional differences in colonization patterns of saproxylic beetle species in a total of 688 fresh deadwood logs of 13 tree species in 9 sites of managed conifer and beech forests, and unmanaged beech forests, respectively. We found that tree species identity was an important driver in determining saproxylic species composition and abundance within fresh deadwood. However, saproxylic species showed different colonization patterns of deadwood items of the same tree species among the study regions. Regionally consistent, conifer forests were most diverse. We attribute the latter result to the historically adaption of saproxylic beetle species to semi-open forests, which conditions are actually best reflected by conifer forests. To preserve a diverse local species pool of early successional saproxylic beetles, we suggest an equal high degree of deadwood diversity in a tree species context in due consideration of regional differences.

Chapter III

The extinction risk of a particular species corresponds with its species-specific requirements on resources and habitat conditions, in other words with the width of the species` ecological niche. Species with a narrow ecological niche are defined as specialists. Members of this group experience higher extinction risk by resource limitation than generalists, which are able to utilize a variety of resources. For the classification of species as specialists or generalists, thus evaluating possible extinction risks, ecologists use the concept of interaction networks. This method has often been applied for mutualistic or antagonistic plant-animal interactions, but information for networks of detritivores is scarce. Therefore, saproxylic beetle species sampled as described in chapter II were categorised according to their larval diet; additionally their interaction networks (N=108) with 13 dead host tree species were analysed. Specialisation degree was highest for wood-digesting beetles and decreased with increasing trophic level. Also the network indices evaluating robustness and generality indicated a higher susceptibility to species extinctions for xylophagous than for mycetophagous and predatory beetles. The specialisation of xylophagous species on specific tree species might be an adaption to tree species specific ingredients stored for defence against pathogens and pests. However, we conclude that the high specialisation degree of xylophages and thus their higher extinction risk by resource loss harbours certain dangers for ecosystem function and stability as species diversity is positively linked to both.

Chapter IV

Populations depend on individual emigration and immigration events to ensure genetic exchange. For successful migration it is of utmost importance that spatially separated populations are obtainable by specimen. Migratory success depends on the one hand on the species dispersal abilities and on the other on the availability of suitable habitats in the surrounding landscape in which the distinct host populations exist. However, consequences of intensive forest management correspond not only to severe reduction of local deadwood amount, but, among others, also a change in tree species composition and high levels of fragmentation in the surrounding forest area. Saproxylic beetle species differ in their dispersal behaviour according to the temporal availability of their preferred habitat. Generally, early successional saproxylic beetles are able to disperse over large distances, whereas beetles inhabiting advanced decayed wood often remain close to their larval habitat. Due to this, environmental factors might affect saproxylic beetle guilds differently. We classified the saproxylic beetles sampled as described in chapter II according to their calculated habitat niche as early, intermediate or late successional saproxylic beetles. For the different guilds the effects of 14 environmental factors on different spatial scales (stand factors at 0.1 km radius, landscape composition at 2 km radius, and regionally differing abiotic factors in 400 km to 700 km distance) were investigated. Consistently for all guilds, species richness decreased with fragmentation at local and landscape scale, and increased in warmer climate. However, we found contradictory results between the guilds to some extent.

We relate this to guild specific habitat requirements of the saproxylic beetles. Therefore, for the development of appropriate conservation practices guild-specific requirements saproxylic beetles have to be considered not only locally but on larger spatial scales.

Chapter V

In conclusion, this dissertation identified main drivers of early successional saproxylic beetle species richness on various spatial scales. Our results emphasize the importance to develop management schemes meeting species-specific and guild-specific habitat requirements of the saproxylic beetle fauna at relevant spatial and temporal scales. Therefore, short-term actions suggested for sustainable forest management should be the focus on a diverse tree species composition consisting of indigenous tree species with respect to regional differences. Moreover, senescent trees, fallen and standing deadwood should remain in the forests, and some tree individuals should be allowed to grow old. Long-term actions should involve the reduction of forest fragmentation and the connection of spatial widely separated forest fragments. Furthermore, to fully understand the effects of forest management long-term research should be conducted to compare habitat requirements of intermediate and late successional beetles with the results presented in this dissertation.

ZUSAMMENFASSUNG

Kapitel I

Die Mineralisierung von toter organischer Materie nimmt eine Schlüsselfunktion innerhalb eines Ökosystems ein, da sie die beiden essentiellen Komponenten des Energie-Nährstoff-Zyklus - Zersetzung und Primärproduktion - miteinander verbindet. Anthropogen bedingte Störungen wie z.B. Arten-, oder Ressourcenverluste können jedoch das Gleichgewicht zwischen den beiden wichtigen Ökosystemdienstleistungen Produktion und Abbau aus der Balance bringen.

Um die Nahrungsversorgung der Menschheit zu gewährleisten, wurde bereits ein großer Teil der Natur in Agrarflächen umgewandelt und die Produktion durch intensive Bewirtschaftungsformen gesteigert. Weltweit gibt es nur noch wenige Gebiete ohne menschliche Beeinflussung. Um dauerhaft essentielle Ökosystemdienstleistungen zu gewährleisten, sind Kenntnisse über die Auswirkungen von intensiver Bewirtschaftung auf das Zusammenspiel zwischen Artenvielfalt und Ökosystemfunktionen unabdingbar.

Der größte Teil der terrestrischen Biomasseproduktion wird von Wäldern geleistet. Obwohl die Waldbewirtschaftung in Europa lange Zeit nachhaltig war, wirkte sich deren Intensivierung während des letzten Jahrhunderts massiv auf die Waldstruktur und die damit assoziierte Fauna aus. Besonders betroffen sind die obligatorisch an Totholz gebundenen Organismen. Innerhalb der Totholzfauna sind xylobionte Käfer eine artenreiche und funktional hoch diverse Gruppe, doch aufgrund von Lebensraumverlusten sind viele Arten stark bedroht. All diese Eigenschaften klassifizieren Totholzkäfer zu idealen Forschungsobjekten, um die Auswirkungen von intensiver Waldbewirtschaftung auf Ökosystemfunktionen zu untersuchen.

Das BELONGDEAD-Projekt hat als Ziel, die funktionalen Auswirkungen von Veränderungen in der Artengemeinschaft auf die Abbauraten von Totholz zu analysieren. Der Untersuchungszeitraum des in Deutschland beheimateten Projekts umfasst die Initialisierung des Zersetzungsprozesses bis zum vollständigen Abbau von experimentell ausgelegten Totholzstämmen unterschiedlicher Baumarten. Als Teil des BELONGDEAD-Projekts lag der Fokus der vorliegenden Dissertation auf der Totholzkäferfauna. Wir untersuchten (1) regionale Effekte der Baumartenzugehörigkeit von frischem Totholz und (2) die Auswirkungen von Waldbewirtschaftung unterschiedlicher Intensität auf die Artenvielfalt, Abundanz und Struktur der Artengemeinschaften von totholzbewohnenden Käfern (Kapitel II); (3) den Spezialisierungsgrad verschiedener trophischer Gilden von Totholzkäfern, sowie die Stabilität und Robustheit ihrer jeweiligen Netzwerke gegen Störungen (Kapitel III); (4) den Einfluss von Umweltfaktoren auf die Artenvielfalt xylobionter Käfergilden auf mehreren räumlichen Skalen.

Kapitel II

Der Großteil der europäischen Wälder ist anthropogen beeinflusst. In Europa bilden Naturwälder weniger als 1% der gesamten Waldfläche von ca. 1 Mrd. Hektar. Traditionelle Waldbewirtschaftung und vor allem der technologische Fortschritt des letzten Jahrhunderts fragmentierten die Waldfläche in hohem Maß, und verursachten beträchtliche Verluste an lebensnotwendigen Ressourcen. Besonders innerhalb der obligatorisch an Totholz gebundenen Gruppe der xylobionten Käfer verzeichnete man einen rasanten Artenrückgang. Daher gab es einen großen Bedarf an Studien, die Untersuchungen zur Mindestmenge an lokal vorhandenem Totholz zur Sicherung der xylobionten Artenvielfalt durchführten. Wenig beachtet wurde bisher jedoch die Bedeutung der Baumartenzugehörigkeit von Totholz für die Besiedlung durch xylobionter Käfer in verschiedenen Waldbewirtschaftungssystemen auf lokaler und regionaler Ebene. Wir untersuchten daher mögliche Unterschiede zwischen 3 Regionen im Besiedlungsmuster xylobionter Käfer bei insgesamt 651 experimentell ausgelegten Baumstämmen in einem frühen Sukzessionsstadium von 13 Baumarten auf jeweils 9 Untersuchungsflächen in bewirtschafteten Buchen- und Nadelwäldern, sowie in unbewirtschafteten Buchenwäldern. Bei den ausgelegten Totholzstämmen war die Baumartenzugehörigkeit ausschlaggebend für die Struktur der Artengemeinschaften und Abundanzen xylobionter Käfer. Aufgrund der unterschiedlichen regionalen Artenpools divergierten die Besiedlungsmuster xylobionter Käferarten von Totholz der gleichen Baumart in den verschiedenen Regionen stark voneinander. In allen Regionen zeigten die Totholzkäfer in Nadelwäldern die höchste Artenvielfalt. Dieses Ergebnis lässt sich auf die - historisch bedingte - Anpassung der Totholzkäferfauna an eine halboffene Waldstruktur zurückführen, die derzeit am besten durch Nadelwälder widergespiegelt wird. Um eine diverse lokale Artengemeinschaft xylobionter Käfer zu gewährleisten ist eine große Variabilität vom baumartspezifischen Totholz unabdingbar, wobei regionale Unterschiede in Betracht gezogen werden müssen.

Kapitel III

Das Aussterberisiko einer Art ist abhängig von den artspezifischen Ansprüchen an ihre Umwelt und den dort vorkommenden Ressourcen –auch definiert als die ökologische Nische der betrachteten Art. Arten mit geringer Nischenbreite sind per definitionem Spezialisten. Mitglieder dieser Gruppe stehen durch Verarmung ihres Ressourcenangebots unter einem höheren Aussterberisiko als Generalisten, die eine größere Variabilität in ihrem Ressourcenspektrum aufweisen. Interaktionsnetzwerke dienen in der Ökologie als wichtiges Werkzeug um das Aussterberisiko spezifischer Arten zu bewerten und eine Einteilung hinsichtlich Spezialist oder Generalist vorzunehmen. Bei mutualistischen oder antagonistischen Tier-Pflanzen-Interaktionen ist diese Methode etabliert, doch für die Gruppe der Zersetzer ist das Netzwerk-Konzept bisher nur sporadisch angewandt worden. Daher teilten wir die xylobionten Käferarten, die im Rahmen des in Kapitel II beschriebenen Experiments gesammelt wurden, anhand ihres larvalen Ernährungstyps in drei trophische Gilden (Xylophage, Mycetophage und Räuber) ein; anschließend wurden ihre Interaktionsnetzwerke (N= 108) mit den 13 Wirtsbaumarten analysiert. Rein xylophage Arten wiesen den höchsten Spezialisierungsgrad auf, der mit zunehmendem trophischem Grad geringer wurde. Die Netzwerkparameter Robustheit und Generalität ließen ebenfalls auf eine höhere Anfälligkeit für Artenverluste bei xylophagen als bei mycetophagen oder räuberischen Arten schließen. Die Spezialisierung xylophager Arten auf spezifische Baumarten ist möglicherweise eine Adaption an artenspezifische sekundäre Inhaltsstoffe, die als Schutz vor Schädlingen und Krankheitserregern in Holz und Rinde gespeichert werden. Der hohe Spezialisierungsgrad xylophager Käfer bedingt ein höheres Aussterberisiko bei Ressourcenverlust. Dies würde die Stabilität des Ökosystems und dessen Ökosystemfunktionen nachhaltig schwächen da eine hohe Artenvielfalt Garant für ein funktionierendes Ökosystem ist.

Kapitel IV

Individuelle Immigrations- und Emigrationsereignisse sind für die Sicherstellung des genetischen Austauschs zwischen Populationen essentiell. Daher ist von größter Wichtigkeit, dass die räumliche Distanz zwischen Populationen von den zu- oder abwandernden Individuen überwunden werden kann. Der Migrationserfolg ist dabei zum einen von der artspezifischen Ausbreitungsfähigkeit, und zum anderen von der Verfügbarkeit an geeigneten Habitaten in der Umgebung der Populationen abhängig. Die Folgen intensiver Waldbewirtschaftung sind jedoch nicht nur ein drastische Verminderung des lokalen Totholzvolumens, sondern unter anderem auch die Veränderung der Baumartengesellschaften, sowie hochgradige Fragmentierung der Waldflächen und der umgebenden Landschaft. Xylobionte Käferarten unterscheiden sich in ihrem Ausbreitungsverhalten hinsichtlich der zeitlichen Verfügbarkeit ihres bevorzugten Habitats. Im Allgemeinen können Besiedler früher Sukzessionsstadien weite Strecken überwinden, wohingegen Bewohner von Alttotholzstrukturen meist nahe ihrem Ursprungshabitat verbleiben. Dies legt die Vermutung nahe, dass Umweltparameter verschieden auf unterschiedliche Habitatgilden einwirken. Um diese Vermutung zu überprüfen, wurde für die gesammelten xylobionten Käferarten ihre jeweilige Habitatnische berechnet. Wir klassifizierten die Arten als Besiedler von entweder frühen, mittleren oder alten Totholzstrukturen. Für jede Gilde wurde der Einfluss von 14 Umweltparametern auf verschiedenen räumlichen Skalen - Standortfaktoren der Untersuchungsfläche (Radius: 100 m), Landschaftsparameter im Umkreis von 2 km der Untersuchungsfläche, sowie regionenspezifische abiotische Faktoren (Distanz zwischen den Regionen: 400 – 700 km) - untersucht. Bei starker lokaler und landschaftlicher Fragmentierung nahmen die Artenzahlen in den xylobionten Gilden ab, während sich höhere Jahresdurchschnittstemperatur positiv auf die Artenvielfalt auswirkte. Jedoch gab es hatten nicht alle Umweltfaktoren den gleichen Effekt auf die Gilden. Wir führen dies auf die unterschiedlichen Habitatansprüche der xylobionten Gilden zurück. Um adäquate Schutzmaßnahmen für Totholzkäfer zu entwickeln, müssen die spezifischen Habitatansprüche der verschiedenen xylobionten Gilden, nicht nur auf lokaler, sondern auch auf größeren räumlichen Ebenen in die Planungen miteinbezogen werden.

Kapitel V

In der vorliegenden Dissertation konnte ich wichtige Triebfedern der Artenvielfalt xylobionter Käfer identifizieren. Unsere Ergebnisse unterstreichen die Notwendigkeit der Entwicklung von nachhaltigen Waldbewirtschaftungskonzepten, die den art- und gildenspezifischen Anforderungen xylobionter Käfer an den Lebensraum auf den relevanten räumlichen und zeitlichen Skalen gerecht werden.

Kurzfristige Maßnahmepläne für eine nachhaltige Forstwirtschaft sollte die Förderung von Mischwäldern mit einer vielfältigen Baumartengemeinschaft mit standortgemäßen einheimischen Hölzern unter Berücksichtigung regionaler Besonderheiten beinhalten. Alte Bäume, sowie liegendes und stehendes Totholz sollten im Wald verbleiben und einzelne Bäume aus der Nutzung genommen werden um die Strukturen altgewachsener Bäume langfristig zu gewährleisten. Langfristige Ziele sind die Verringerung der Waldfragmentierung und das Anlegen von Biotopverbundsystemen, um weit auseinanderliegende Waldflächen wieder miteinander zu verbinden. Um die Auswirkungen kommerzieller Forstwirtschaft im vollen Umfang zu erfassen, sind Langzeitstudien notwendig die die Habitatansprüche xylobionter Käfer aus mittleren und alten Totholzsukzessionsstadien mit den Ergebnissen der vorliegenden Dissertation vergleichen.

CHAPTER 1: GENERAL INTRODUCTION

Life is based on decomposition

Asked for the basis for life on earth, the often given answer is photosynthesis. Via photosynthesis, autotrophs (all kinds of green plants) convert atmospheric carbon dioxide (CO_2) in energy-rich biomass, upon heterotrophs (global fauna, including most fungi, bacteria, and protozoa) ultimately depend (Krebs 2009). Annually, primary producers remove 120 Pg (1 Pg = 10^{15}g) of CO_2 from the atmospheric carbon stock and convert it to 67 Pg of dry biomass (Malhi 2002; Banerjee *et al.* 2012). This process is observable every spring by plant growth, or by deciduous trees coming into leaf.

However, for the composition of energy-rich organic matter, not only CO_2 is essential, but also mineral nutrients, e.g. nitrogen (N) or phosphor (P). Contrary to the atmospheric carbon stock, mineral nutrients are stored in the soil via decomposition of dead organic matter (Bobiec *et al.* 2005). The process of decomposition is defined as the gradual degradation of dead organic material resulting in energy release and the conversion of organic molecules in inorganic elements (Begon *et al.* 2006). Globally, consumers of dead organic matter comprising decomposers (fungi and bacteria) and detritivores (animals feeding on dead organic material), annually turn 50% of the formed biomass into essential inorganic minerals for the autotrophs, thereby completing the nutrient cycle (Lal 2008; Krebs 2009). Due to the fact that plant-growth is often limited due to a shortened availability of nitrogen and phosphor, decomposition is among the most important processes for sustaining life on earth (Bobiec *et al.* 2005).

Therefore, to ensure biomass production by primary producers, a balanced system between the amount of composed dead organic material and the activity of decomposers and detritivores must be maintained. The generally observed positive effect of overall high species diversity on the maintenance of key ecosystem processes such as primary productivity and decomposition resulted in the ecological insurance-hypothesis, which states that ecosystem functions are able to be resumed by a diverse species pool due to functional redundancy, if present species go extinct (Yachi & Loreau 1999). Moreover, a highly diverse ecosystem is assumed to be less prone to disturbances than species-poor ones (Krebs 2009).

Forests – more than just trees

On earth, forests form one of the oldest and largest vegetational systems. One third (3,9 milliard hectare) of land mass are currently covered by forests (FAO & JRC 2012), and fossilized forests are known from the mid-Devonian (Roversi & Nannelli 2012).

The main features of natural forests are spatial heterogeneity generated by a diverse tree species composition and multi-layered structure (Merganičová *et al.* 2012). Furthermore, the maintenance of temporal variability in terms of tree age class distribution and a continuous supply of deadwood at various decay stages created by succession and natural disturbances, such as windthrow, lightning or snow-breakage (Hjältén *et al.* 2012).

However, forests are not only assemblages of tree individuals, but form ecosystems with distinct microclimate, biotic and abiotic characteristics, as well as an associated flora and fauna (Bobiec *et al.* 2005). For humans, forests provide some essential ecosystem services, e.g. air purification, provision of clean water and water retention (Bengtsson *et al.* 2000; Foley *et al.* 2005; Kremen 2005). Moreover, forests are the most productive terrestrial ecosystem (Luyssaert *et al.* 2007). Per year, 40 Pg of carbon are fixed in forest vegetation, thereby contributing the largest proportion of the globally primary production (Scherer-Lorenzen *et al.* 2005). The vast majority of nutrients is stored in woody material, e.g. 1 m^3 of oak wood contains 0,3 kg of potassium and 0,1 kg of sodium and phosphor, respectively (Bobiec *et al.* 2005). However, most of forest living biomass becomes incorporated in dead organic material, thus the key process for the maintenance of nutrient cycling and for sustaining forest ecosystem functions is the decomposition of deadwood material (Ulyshen 2013). Furthermore, deadwood has substantial ecological value as key for the maintenance of forest biodiversity (e.g. Janssen *et al.* 2011; Djupström *et al.* 2012; Ulyshen 2013). Up to 50 % of forest biota worldwide is obligatory deadwood depending. Therefore, the withdrawal of deadwood, thereby limiting and eliminating essential habitats and nutrient resources is expected to have severe consequences for forest diversity and essential ecosystem functions (Lassauce *et al.* 2012).

Forest management and its consequences

In Europe, natural forests account for less than 1 % of the about 1 milliard hectare of forest area and might exclusively be found in the Polish Białowieża National Park (Bobiec 2002).

Thus, almost every European forest has been anthropogenically manipulated in the past, or is under current management. For centuries, forestry was concentrated near human settlings, e.g. for cutting of firewood and timber, and conversion of forest area into agricultural land, thus causing continued forest fragmentation (Bengtsson *et al.* 2000; Müller *et al.* 2012). However, within the last century, forest practices, and thus human impact increased rapidly due to advances in technology. The effects of modern forestry on forest ecosystems are: change from a diverse tree species composition and age distribution to even-aged monocultures, accompanied by a decline of structural variability in a spatial and temporal context (Koch Widerberg *et al.* 2012; Lassauce *et al.* 2012; Gossner *et al.* 2013), the suppression of natural succession which has led to a lack of free-standing veteran trees (Bouget *et al.* 2012), and, probably most critical for forest biota and productivity, dramatic decrease of average deadwood volume on forest sites from 130 - 500 m^3ha^{-1} to 1-23 m^3ha^{-1} during the last century (Bobiec *et al.* 2005; Merganičová *et al.* 2012). Especially large diameter wood has been removed, on the one hand on the pretext of public safety (Hjältén *et al.* 2012). On the other hand it was assumed that well-decayed lying or standing deadwood is a potential source of pathogens and pests (Väisänen *et al.* 1993). However, by removing of deadwood not only essential habitat, but also nutrients are lost for the forest ecosystem. It has been estimated that by a continuous extraction of 400 m^3 of oak deadwood from just one hectare during 100 years, about 126 kg of potassium, 45 kg of sodium, 36 kg of magnesium, 803 kg of calcium, and 40 kg of phosphor is lost for the forest nutrient storage (Bobiec *et al.* 2005). Moreover, the rapid decline of deadwood amount has been identified as one key factor for forest biodiversity loss. However, the recently demand for biofuels has again increased pressure on conservation practices aiming at an increased deadwood supply left on forest sites (Lassauce *et al.* 2012; Müller *et al.* 2012).

Saproxylic beetles as indicators for biodiversity loss

In Europe, saproxylic organisms, which comprises species of many taxa, e.g. birds, lichens, mosses, fungi, molluscs, and arthropods, suffered the most severe species losses due to the extreme reduction of available deadwood amount (Müller *et al.* 2007; Vodka *et al.* 2008). Generally, saproxylics are defined as organisms which depend on dead or dying wood at least at one stage of their life (Speight 1989). This dissertation focusses on the group of saproxylic beetles, which are beside fungi the most species rich group among saproxylic organisms.

In Germany, 1,378 of the 6,600 domestic beetle species are classified as saproxylic (Köhler 2000). Furthermore, the excellent knowledge about species ecology and their high functional diversity qualify them as ideal research organisms (Jonsell 2008; Müller *et al.* 2012). Saproxylic beetles can be found in all decay stages of deadwood, thereby fulfilling fundamental roles as ecosystem engineers. Saproxylic beetles colonizing fresh deadwood initiate the decomposition process by the mechanical break-down of woody material by gnawing and boring and by creating entry holes for later successional saproxylic organisms, as well as for water and air. Furthermore, they directly and indirectly disperse wood decaying fungi, thereby initialising fungal growth (Speight 1989; Martikainen *et al.* 1999; Vanderwel *et al.* 2006; Nieto & Alexander 2010; Quinto *et al.* 2012). Later successional saproxylic beetles continue wood decay by dislocating nutrients from woody detritus, thereby granting access for nitrogen-fixing bacteria and mineralizing micro-organisms (Roversi & Nannelli 2012). Thus, saproxylic beetles actively contribute to forest productivity as well as stability. Hence, the ecological influence of saproxylic beetles exceeds their effects on wood decay (Ulyshen 2013). Due to their dependence on deadwood, saproxylic beetles are most sensitive to disturbances and structural habitat changes caused by forest management practices (Gibb *et al.* 2006b). Furthermore, saproxylic beetles serve as umbrella group, as their vulnerability to intensive forest management is exemplary for other saproxylic organisms (Sobek *et al.* 2009; Müller *et al.* 2012).

Since noticing that saproxylic beetles are suffering from severe species losses due to management intensification, near-to-nature management methods, e.g. selective cutting instead of clear-cutting, natural regeneration, and promotion of native tree composition have been established during the last decade (Gossner *et al.* 2013). However, these procedures revealed to be insufficient as a conservation-oriented method as in respect to forest economic viability, the amount of deadwood of large diameter and in late decay stages is still reduced (Müller *et al.* 2012; Gossner *et al.* 2013). The still ongoing decline caused the actual appearance of 14 % of all European saproxylic beetle species on the European Red Lists (Grove 2002b; Nieto & Alexander 2010).

The Biodiversity Exploratories

Ecologists aim to understand the distributions of biota and their interactions with the ecosystem they live in (Begon *et al.* 2006). As ecosystems with their associated fauna are too complex to be investigated as a whole, a constructive approach is to pick out partial aspects for drawing conclusions about ecosystem functioning. This dissertation was part of the Biodiversity Exploratories, a research project funded by the German Science Foundation (DFG Priority Program 1374), serving as an open research platform (Fischer *et al.* 2010). Three study regions across Germany were established: the UNESCO Biosphere Reserve Schorfheide-Chorin (SCH) in Brandenburg, the Hainich-Dün area (HAI) with the UNESCO World Heritage Site National Park Hainich in Thuringia, and the UNESCO Biosphere Reserve Swabian Alb (ALB) located in Baden-Württemberg (Figure I.1). In each region, 100 plots, 50 in grassland and 50 in forests were selected for experimental manipulations and biodiversity monitoring. Out of the 50 experimental plots (EP) 9 study plots (the so called Very-Intensive-Plots (VIP)) in grassland and forests respectively, were chosen for detailed and labour-intensive investigations (Figure I.1).

BELONGDEAD-Experiment

Forest management practises has led to an impoverishment of saproxylic fauna (Siitonen & Martikainen 1994; Martikainen *et al.* 2000; Grove 2002b). Therefore, the long-term project BELONGDEAD was established at 30 forest VIPs to investigate effects of intensified forest management on the processes and taxa involved in deadwood decomposition.

For the BELONGDEAD-experiment three types of management intensities (nine replicates per forest management intensity) were selected: (1) unmanaged European beech (*Fagus sylvatica*) dominated forest sites, (2) managed age-class beech (*F. sylvatica*) forest sites harvested at 80 – 120 year intervals, and (3) intensively managed conifer age-class forest sites, which is spruce (*Picea abies*) in Hainch-Dün and Swabian Alb, and pine (*Pinus sylvestris*) in Schorfheide-Chorin (chapter II, III, and IV).

As different host tree species address complementary saproxylic species of the local coleopteran species pool (Lindhe & Lindelöw 2004), freshly logged deadwood logs of 13 tree species (*Acer* sp., *Betula pendula, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus* sp., *Prunus avium, Pseudotsuga* *menziesii*, *Quercus* sp., *Tilia* sp.) were experimentally exposed in random order on each 1 ha research plot to investigate the relevance of host tree identity for saproxylic beetles (Fig. I.2; chapter II and III).

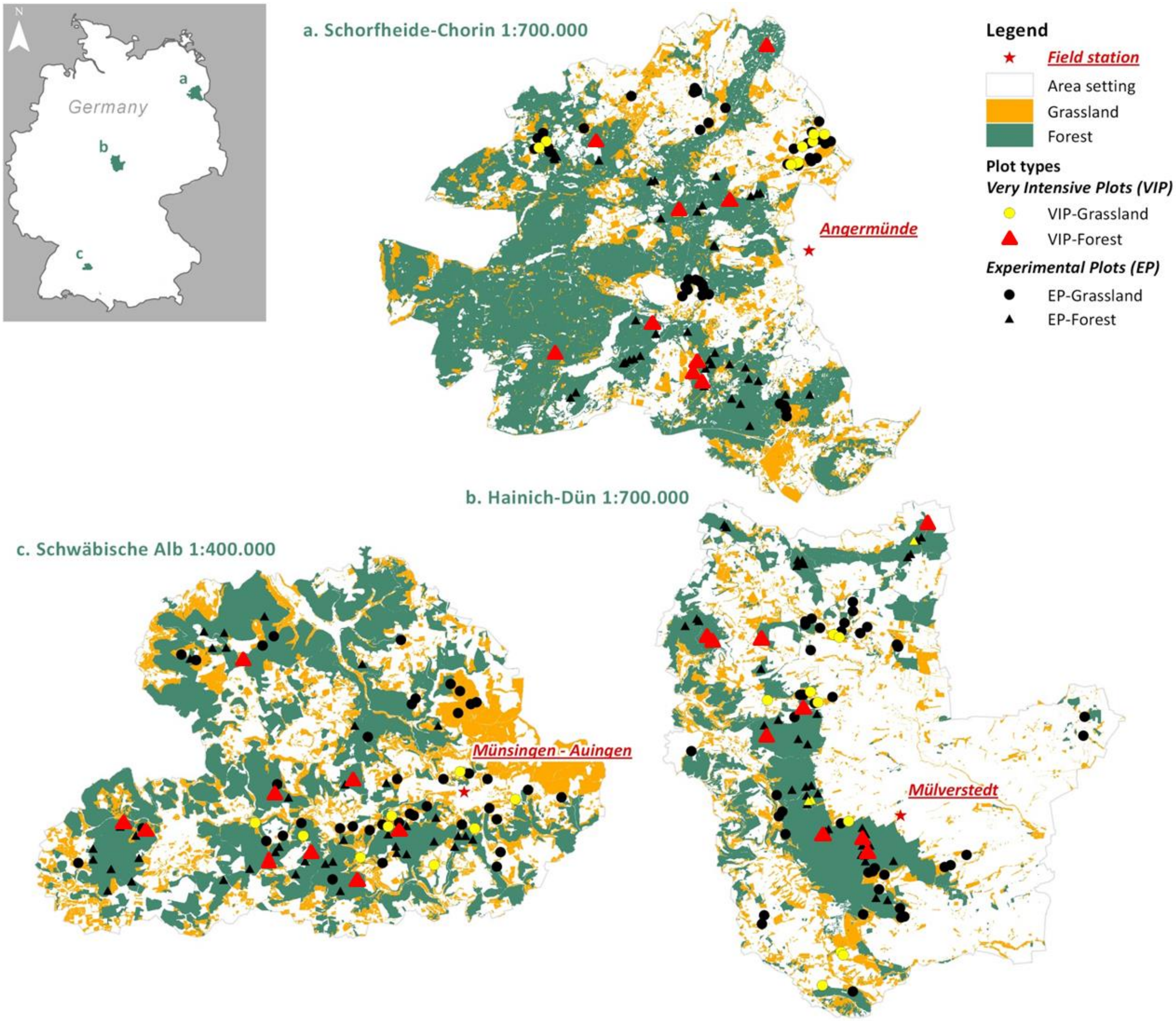


Fig. I.1: Locations of the EPs and VIPs within the study regions (a) Schorfheide-Chorin, (b) Hainich-Dün, and (c) Swabian Alb. Red triangles mark the selected study plots for the experiments conducted in this thesis.

Sampling of saproxylic beetles

For the monitoring of deadwood colonization by saproxylic beetles overall 688 logs (229 in ALB and HAI, 230 in SCH) were equipped with closed emergence eclectors, a standardised method for the sampling of saproxylic beetles (Alinvi *et al.* 2006). The eclectors were built up of a curved metal rail (width 32 cm) and a panel of black cotton on each side. For sampling, eclectors were screwed on the deadwood logs and sealed with polyurethane foam. A sampling jar was mounted on top and two smaller ones were installed at both ends of the metal rail. Each jar was filled with saturated NaCl-solution (Fig. I.2). Traps were installed in March 2011 before the beginning of the seasonal activity of saproxylic beetles, emptied monthly, until the end of saproxylic seasonal activity at the end of September 2011. Sample material was stored in 70 % Ethanol. Beetles were sorted out in the lab and determined to species level by taxonomic specialists.

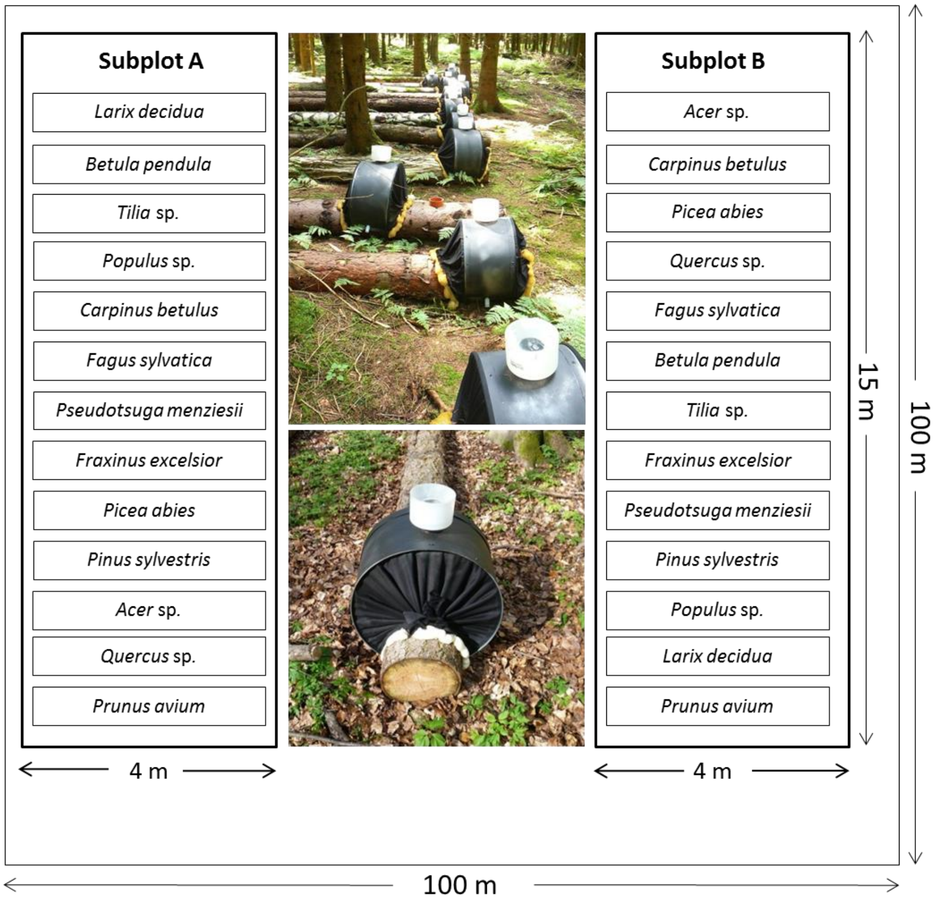


Fig. I.2: General experimental set-up.

Saproxylic beetle guilds

Apart from taxonomic classification saproxylic beetles could be grouped into guilds, i.e. groups of organisms using the same ecological resource (Root 1967; Hawkins & MacMahon 1989). Based on their nutritional ecology saproxylic beetle species were distinguished between (1) primary consumers of woody material, (2) consumers of fungi and mouldy material, and (3) saproxylic beetles preying on other saproxylic organisms to evaluate the dependence of trophic beetle guilds on host tree identity (chapter III). Furthermore, beside their nutritional ecology, each saproxylic beetle species preferably inhabit deadwood of a specific decay stage. Therefore, by recording habitat information, the niche position for each beetle species across the decay stages can be calculated (Gossner *et al.* 2013). We classified the sampled saproxylic species according to their calculated niche position as either fresh deadwood inhabiting or advanced decayed wood inhabiting beetles (chapter IV).

Environmental parameters

Environmental factors on stand and landscape level as well as local and regional climate parameters are known to influence species pool of saproxylic beetles (Okland *et al.* 1996; Franc & Götmark 2008). In total we investigated 14 parameters at three different spatial scales (0.1 km radius, 2 km radius, and 400 km to 700 km distance) for their effects on overall species richness and diversity of saproxylic beetles, as well as for saproxylic beetles preferably inhabiting either fresh or advanced decayed deadwood (chapter IV).

CHAPTER II: SAPROXYLIC BEETLE DIVERSITY IN TEMPERATE FORESTS:

EFFECTS OF TREE SPECIES IDENTITY, MANAGEMENT AND GEOGRAPHIC REGION

Abstract

The endangered status of increasing numbers of deadwood inhabiting beetle species due to large-scale and long-term forestry indicates that current conservation practices are insufficient in central Europe. Therefore, we investigated via a large-scale experiment whether tree species identity and diversity, forest management or regional variation is more important for saproxylic beetle diversity. In three distinct regions in Germany we exposed 1025 deadwood logs comprising 13 tree species and studied the diversity of saproxylic beetles in 27 forest sites of three management types. Saproxylic beetle species richness differed between tree species, management types, and regions. The interaction between tree identity and study region indicates context-dependent effects on saproxylic beetle species richness. Multiplicative partitioning of saproxylic beetle diversity indicated that observed alpha-diversity within logs was lower and beta-diversity mostly higher than a random distribution of species. The importance of beta-diversity was equal among the considered spatial scales, suggesting that besides tree species, also management types and regions hosted distinct beetle communities. Deadwood of the regional main tree species (beech, spruce, pine) maintained about 50 % of the local saproxylic beetles species pool and about nine different tree species were necessary to support 90 % of the regionally detected saproxylic beetle species. We conclude that conservation of saproxylic beetle communities in central Europe needs novel management approaches which enhance the diversity of deadwood in a tree species context but regional variation in the relative effectiveness of different tree species to support high saproxylic beetle diversity must be taken into account.

Keywords

Coleoptera; deadwood; decomposition; conifer forests; forest ecology; land use intensity; conservation practices; emergence traps

Introduction

In Europe, 40 % of the land mass (1 milliard hectare) are covered by forests, but less than 1% of these are classified as primeval (Bobiec 2002; Parviainen 2005; Paillet *et al.* 2010). During the last century rapid changes in forestry due to advanced technologies have led to drastic effects on tree composition as well as stand and age structure of previously natural forests (Bengtsson *et al.* 2000). Modern forestry caused the conversion of structurally variable and multi-layered woodlands in even-aged and mono-layered forests (Hjältén *et al.* 2007; Paillet *et al.* 2010).

As deadwood is a key element for sustaining forest biodiversity, especially the removal of senescent trees and well-decayed logs caused drastic declines of the associated fauna (Lemperiere & Marage 2010; Janssen *et al.* 2011). The increasing conservation concern for saproxylic, i.e. deadwood inhabiting, species over the last two decades caused a reform of forestry including deadwood retention after logging and non-removal of naturally fallen trees (Jonsell *et al.* 2007; Brunet & Isacsson 2009). However, the recently rising demand for renewable energy resources impairs these conservation efforts (Lassauce *et al.* 2012).

Saproxylic beetles are crucial for initiating and maintaining the decomposition process of woody material and nutrient cycling in forest ecosystems as most nutrients are stored in deadwood (Speight 1989; Bobiec *et al.* 2005; Nieto & Alexander 2010; Ulyshen 2013). The ongoing loss of saproxylic beetle species richness and possible consequences for forest ecosystems have been in the focus of studies worldwide (Saint-Germain *et al.* 2004; Baselga 2008; Paillet *et al.* 2010; Azeria *et al.* 2012). However, in Europe most research has taken place in boreal forests of Fennoscandia, (Djupström *et al.* 2008; Franc & Götmark 2008; Laaksonen *et al.* 2008), whereas studies from temperate forests are still scarce (Lassauce *et al.* 2011, 2012).

In contrast to Fennoscandia, forest management in Central Europe has a long history of sustainable silviculture, but studies document that even near to nature management practises lead to decreasing saproxylic beetle richness, accompanied by a change in functional composition (Gossner *et al.* 2013). To develop effective conservation strategies it is important to identify the parameters which promote saproxylic diversity. For the maintenance of a diverse saproxylic beetle fauna deadwood features such as diameter and decay class are important (Vanderwel *et al.* 2006; Brin *et al.* 2010; Lemperiere & Marage 2010; Bouget *et* *al.* 2012). Until recently, the importance of host tree identity have been rarely studied (Lindhe & Lindelöw 2004). Logs of broadleaved tree species are known to host a distinct saproxylic fauna than coniferous deadwood, but knowledge about species-specific associations of saproxylic beetles with host trees are scarce (Jonsell *et al.* 2007; Saint-Germain *et al.* 2007; Jonsell 2008). Beyond that little is known about local or regional variation in saproxylic diversity, although this has to be key point for successful conservation strategies (Bengtsson *et al.* 2000).

To maintain saproxylic diversity, recent near-to-nature forestry retains deadwood after logging events which might serve as keystone habitat (Djupström *et al.* 2012; Gossner *et al.* 2013). In temperate managed forests, retained deadwood consists of the dominant tree species, usually *F. sylvatica, P. abies, or P. sylvestris*, respectively. However, deadwood of other tree species could play an important role for saproxylic species diversity, but this aspect has been disregarded so far. Deadwood of certain tree species (e.g. oak) might be more attractive for saproxylic beetles and therefore valuable for conservation aspects (Lindhe & Lindelöw 2004; Jonsell *et al.* 2007; Lindbladh *et al.* 2007). It is known that saproxylic species show different degrees of host specificity, with a general trend of decreasing host specificity with advanced stages of decomposition (Speight 1989).

Therefore, we focussed on the early decomposition process and investigated the combined effects of deadwood identity, local forest management, and regional variation on saproxylic beetles colonising experimentally deployed deadwood logs of 13 tree species, including both broadleaf and coniferous tree species. We aimed to identify the key drivers of saproxylic diversity to deduce conservation guidelines for sustainable forest management.

More specifically, we asked (1) whether deadwood of common tree species, e.g. beech, spruce, and pine supports higher numbers of saproxylic beetle species than deadwood of rare tree species; (2) whether different tree species support different saproxylic beetle species; (3) how different intensities of local forest management and (4) geographic regions affect saproxylic beetle diversity.

Material and methods

Study area

Our study was conducted in the framework of the Biodiversity Exploratories (www.biodiversity-exploratories.de). The study regions were located in the glacially formed UNESCO Biosphere Reserve Schorfheide-Chorin (SCH) located in the lowlands (3-140 m a.s.l.) in the North-East (longitudes 14.1° E to 13.4° W, latitudes 53.2° N to 52.8° S); in the Hainich-Dün area (285-550 m a.s.l.) including the UNESCO World Heritage Site National Park Hainich (HAI) in the hilly lands of Central Germany (285-550 m a.s.l.; longitudes 10.8° E to 10.2° W, latitudes 53.4° N to 50.9° S); and the UNESCO Biosphere Reserve Swabian Alb (ALB) located in the low mountain range (460-860 m a.sl) in the South-West (longitudes 6.6° E to 9.2° W, latitudes 48.5° N to 48.3° S) of Germany. Across the three study regions the most frequent tree species was European beech (*Fagus sylvatica*), followed by spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Pine forests occurred only in Schorfheide-Chorin, whereas spruce forests were restricted to the Hainich-Dün and the Swabian Alb (Fischer *et al.* 2010). For more detailed information see www.biodiversity-exploratories.de. In 2012 a forest inventory of the study plots, based on five circular sampling subplots (r= 12,62 m) per study plot was conducted and the tree composition recorded (Schall & Ammer 2013).

BELONGDEAD-Experiment

The BELONGDEAD-Experiment is a long-term experiment for the monitoring of deadwood decomposition. In each study region nine 1 ha research plots from three different managed forest types were chosen: (1) unmanaged beech dominated forest sites, which have been taken out of management 10 to 60 years ago, (2) managed beech forest sites, which are harvested at 80 – 120 year intervals, and (3) conifer plantations, which is spruce in HAI and ALB, and pine in SCH (Fischer *et al.* 2010). In 2009 on each of three subplots per research plot freshly logged (winter 2008/2009) deadwood logs of 13 different tree species (*Acer* sp., *Betula pendula, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus* sp., *Prunus avium, Pseudotsuga menziesii, Quercus* sp., *Tilia* sp.) were placed in random order (Fig. II.1). Two of the three subplots were for experimental manipulations; the third is used as a control. Overall, on the 27 study sites 1,025 deadwood logs (342 logs in SCH and the ALB, 341 logs in HAI) were displayed. Due to a shortage of *Prunus avium* overall 25 logs were missing*:* 9 in ALB (5 on experimental subplots, 4 on control subplots); 7 in HAI (3 on experimental subplots, 4 on control subplots); 9 in SCH (4 on experimental subplots, 5 on control subplots). For the same reason 3 logs of *Acer sp*. were missing on two experimental subplots and on one control subplot in HAI. The exact numbers of logs per local forest management type and regions are given in Appendix II.A; Tab. A.1. To minimize possible effects due to variation of origin, all logs (length of 4 m and diameter between 20 cm to 70 cm) were cut in the state of Thuringia and transported to all study plots.

Sampling of saproxylic beetles

For sampling of saproxylic beetles we used closed emergence eclectors (Fig. II.1). Compared to flight interception traps and trunk-window traps, they are very selective and capture only species emerging from the deadwood logs. Furthermore, eclectors are a non-invasive method, contrasting to woody debris dissection, and the deadwood has not to be removed from forest sites as it is necessary for ex situ rearing (Alinvi *et al.* 2006).

The eclectors were built up of a curved metal rail (width 32 cm) with a panel of black cotton on each side of the metal rail to allow some air circulation beneath the trap. The eclector was screwed on the deadwood log and sealed with polyurethane foam. A sampling jar with a transparent lid filled with saturated NaCl-solution was mounted on top of the trap for the catching of light-attracted species. Additionally, two smaller sampling jars were placed on each end of the metal rail for the catching of bark crawling species (Fig. II.1).We installed emergence traps on all logs (N=688) of the experimental subplots in spring 2011. All deadwood logs were in decay class II – bark and texture intact, original colour of wood- after classification of Bobiec et al. (2005). Traps were emptied monthly from the beginning of April until end of September 2011 and the sample material was stored in 70 % Ethanol. Beetles were sorted out in the lab and determined to species level by taxonomic specialists.

We excluded non-saproxylic beetles from all statistical analyses, which made up 7 % of the total amount. The classification in saproxylic beetles and non-saproxylic beetle species followed Köhler (2000) supplemented by Schmidl and Bussler (2004). Red-listed saproxylic species were classified after Schmidl and Büche (2014). Due to storm we lost many samples in August and September 2011. As the number of saproxylic beetle individuals caught in

August (N=1354) and September (N=508) made up only 5 % of the total amount, we decided to exclude all samples taken in August and September. Furthermore, we had to exclude all samples of study plot 03 in the Swabian Alb due to storm damage in May 2011. In the Swabian Alb three logs of *Pseudotsuga menziesii*, one log of *Carpinus betulus* and *Fagus sylvatica* were excluded because mice gnawed holes in the panels of the trap. For the same reason we had to exclude samples of one log of *F. sylvatica*, *Betula pendula*, and *Picea abies* taken in Hainich-Dün. For analyses, we pooled all samples from the beginning of April until end of July 2011 of the closed emergence traps for each log.

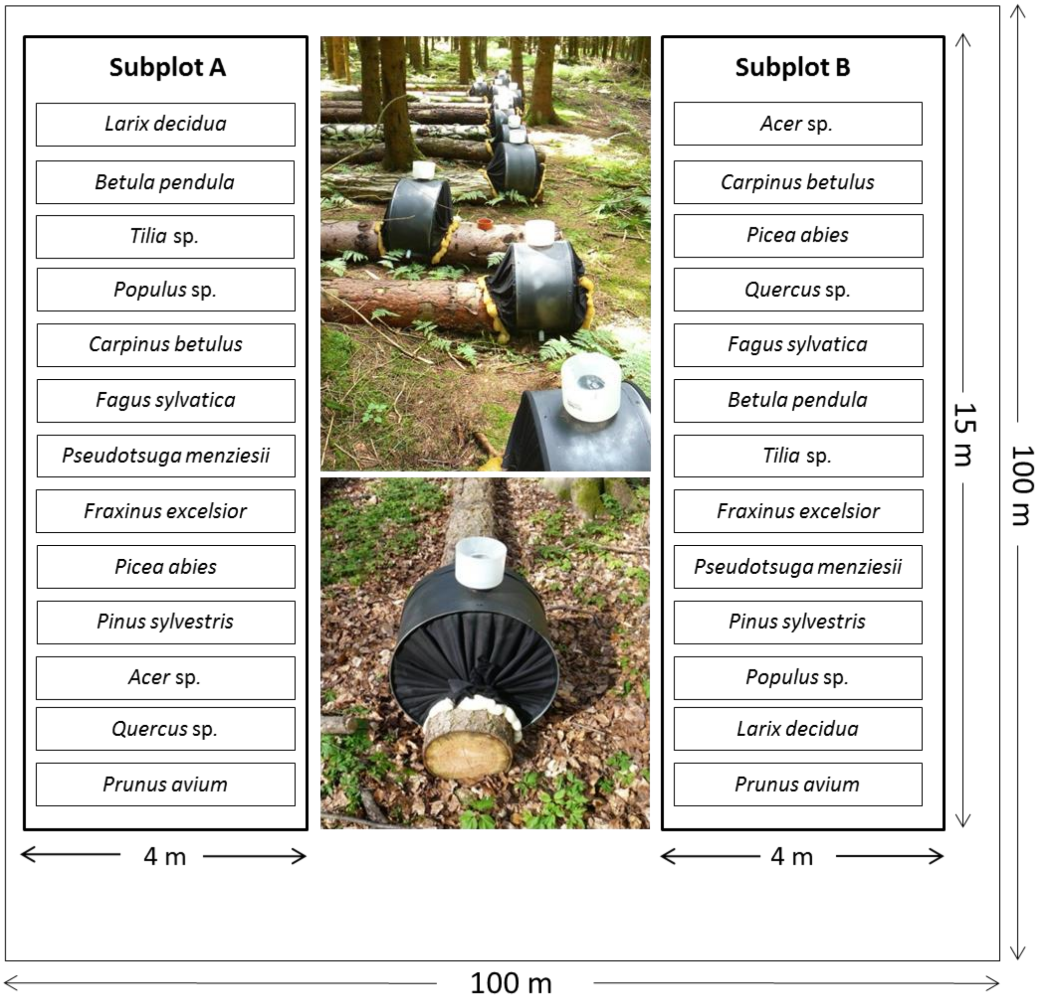


Fig. II.1: General plot design.

Statistics

All statistical analyses were performed with the free software R (R Core Team 2013)**.** Due to differences in log diameter, the surface area covered by emergence traps slightly differed between logs. The total number of individuals sampled per trap strongly correlated with the number of individuals, when corrected for the area covered by the traps (all logs, $R^2 > 0.98$). Therefore, we assume bias due to differences in sample area to be negligible, and thus calculated species richness of saproxylic beetles as the total number of species caught per log.

A Mantel test (package vegan; Oksanen et al., 2009) with 999 permutations was performed to check for spatial autocorrelation for close-by study plots. We correlated spatial distance (degree of latitude and longitude) of each plot with the saproxylic beetle community dissimilarity matrix per study plot using the Bray-Curtis dissimilarity and the Euclidean distance for the spatial variability.

To test whether (1) tree species identity, (2) management type, (3) study region and possible interactions of these parameters had a significant effect on saproxylic species richness and abundance, we calculated a linear mixed effect model (package nlme; Pinheiro et al., 2013). In the model, tree species, local management, study region and their interactions were included as fixed effects and plot, and subplot as random effects. Model simplifications were conducted via stepwise deletion of least significant terms, starting with the three-way interactions, according to Crawley (2007). To pinpoint differences of saproxylic species richness between the different tree species, management types, and study regions we calculated linear mixed effects models, including the random factors plot and subplot, followed by post-hoc Tukey test for multiple comparisons of means (package multcomp; Hothorn et al., 2008).

We calculated the proportion of the local species pool hosted by the main tree species (*F. sylvatica* and *P. abies* in ALB and HAI; *F. sylvatica* and *P. sylvestris* in SCH). By stepwise adding samples of tree species according to their proportion of the stand tree species composition we calculated how many tree species are needed to support all detected saproxylic beetle species.

We used multiplicative diversity partitioning (Whittaker 1960), to partition gamma-diversity into independent alpha- and beta-diversity components as suggested by (Jost 2006, 2007).

Therefore, we used the function “multipart” in vegan package (Oksanen *et al.* 2009). To analyse diversity patterns we used the q-metric with different weighting of rare and abundant species by using three different q-values (Hill 1973; Jost 2007; Chao *et al.* 2014) : (1) q = 0 corresponds to species richness; rare and abundant species in the community are equally weighted here; (2) q = 0.999 (and not q = 1, which would require division by zero) corresponds to the exponential of Shannon entropy; here, species are weighted in proportion to their frequency in the sampled community; (3) q = 2 corresponds to the inverse Simpson concentration; here, abundant species are favoured and rare species are discounted (Chao & Jost 2012). The statistical significance of level-specific alpha and beta estimates was tested using an unrestricted individual-based randomization procedure. In this process 10,000 random distributions of species among samples were generated at all hierarchical levels. Each of the original level-specific estimates was then compared with the appropriate null distribution to test the null hypothesis that the observed alpha- and beta-diversity are obtained by a random distribution of individuals among samples at all hierarchical levels. Statistical significance was assessed by the proportion of null values that are greater than (or smaller than) the actual estimate (Manly 1997; Roff 2006).

To contrast saproxylic beetle communities between forest types and study regions we used Nonmetric Multidimensional Scaling (NMDS) with Bray-Curtis-dissimilarity as distance matrix (package vegan; (Oksanen *et al.* 2013). Prior to this analysis, data of the sampled saproxylic beetle species were pooled for each tree species per study plot. Function *envfit* of the vegan package fits environmental variables onto an ordination. The significance of the goodness of fit is tested via permutations of the environmental variables (Oksanen 2009). We used 999 permutations to test the significance of tree species identity, forest management type, and study region.

Results

Overall, we caught 37,830 saproxylic beetles representing 323 species and 54 families on deadwood logs (N=651) of 13 tree species. We sampled the highest abundance of saproxylic beetles in Hainich-Dün (15,614), followed by Schorfheide-Chorin (12,395) and the Swabian Alb (9,821), whereas more species were found in Schorfheide-Chorin (264), than in Hainich-Dün (143) and on the Swabian Alb (107). Overall, we found 37 red-listed saproxylic beetle species with 31 species in SCH, 8 species in HAI, and 4 in ALB. We found no spatial autocorrelation for close-by study plots in the Swabian Alb (Mantel test, p=0.195), Hainich-Dün (Mantel test, p= 0.205) and Schorfheide-Chorin (Mantel test, p=0.548). Species richness of saproxylic beetles was affected by tree species identity, forest management and region (Tab. II.1). Similarly, abundance of saproxylic beetles differed among deadwood of different tree species and forest management types (Tab. II.1). The interaction of tree species and region indicates that the identity of tree species had different effects on species richness and abundance of saproxylic beetles depending on the regional context; whereas interactions of forest management type with tree species or region were not significant (Tab.II.1).

Tab. II.1: Linear mixed effect models for species richness and abundance of saproxylic beetles including all relevant covariates and interaction terms after model simplification. Significant factors are in bold.

	NumDf	DenDf	F-value	p-value
Species number				
Tree species	**12**	**491**	**17.79**	**<0.0001**
Management	**2**	**17**	**14.49**	**0.0002**
Region	**2**	**17**	**36.86**	**<0.0001**
Tree species : Management	24	491	1.00	0.4628
Tree species : Region	**24**	**491**	**2.00**	**0.0035**
Management : Region	4	17	1.26	0.3236
Tree species : Management : Region	48	491	1.38	0.0505
Abundance				
Tree species	**12**	**491**	**22.67**	**<0.0001**
Management	**2**	**17**	**6.81**	**0.0067**
Region	2	17	0.81	0.2953
Tree species : Management	24	491	1.14	0.2953
Tree species : Region	**24**	**491**	**3.24**	**<0.0001**
Management : Region	4	17	1.75	0.1850
Tree species : Management : Region	48	491	1.23	0.1489

In all regions logs of *C. betulus* were among the most species rich. On the Swabian Alb logs of *Acer* sp. and *Quercus* sp. additionally hosted a diverse saproxylic beetle fauna, whereas in Hainich-Dün deadwood of *P. avium, Acer* sp. and in Schorfheide-Chorin *B. pendula, P. avium* and *Populus* sp. contributed to saproxylic diversity (Fig. II.2).

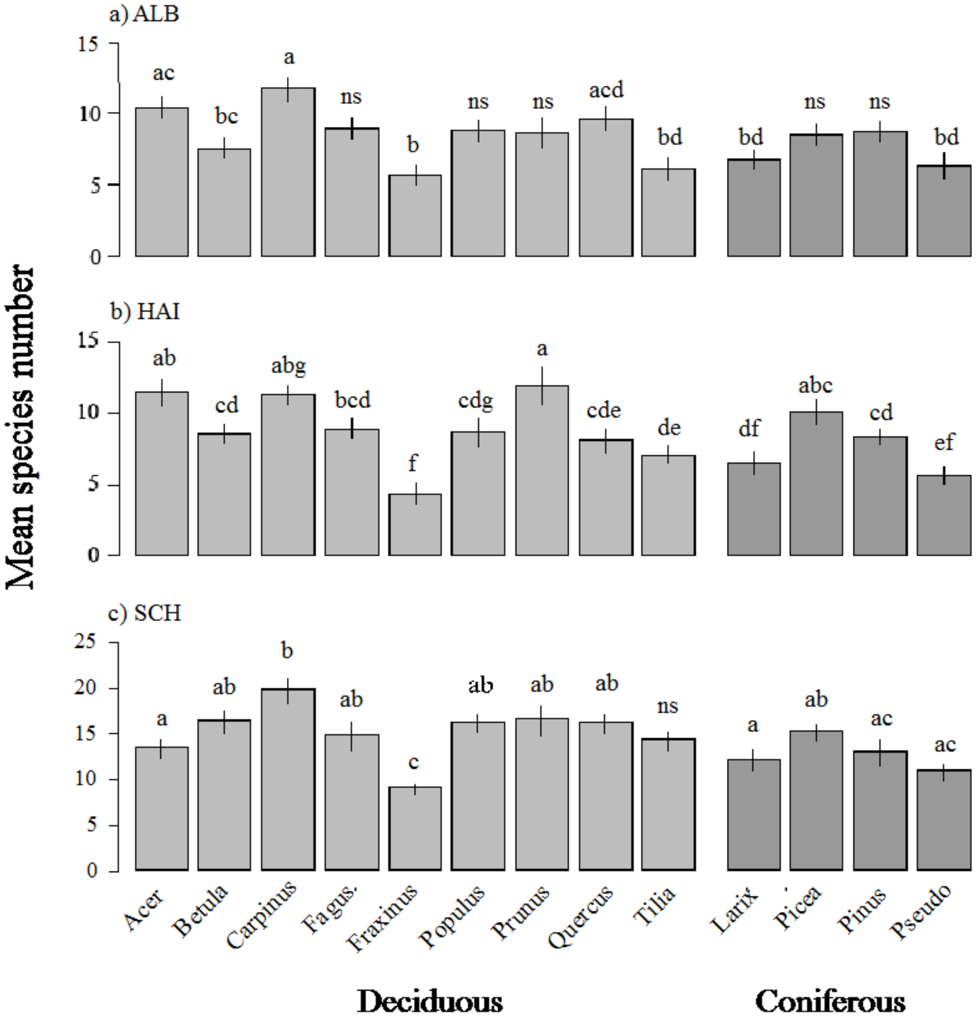


Fig. II.2: Comparison of saproxylic beetle species richness of a) Swabian Alb, b) Hainich-Dün and c) Schorfheide-Chorin between deadwood of different tree species for Acer: *Acer* sp.; Betula: *Betula pendula*; Carpinus: *Carpinus betulus*; Fagus: *Fagus sylvatica*; Fraxinus: *Fraxinus excelsior*; Larix: *Larix decidua*; Picea: *Picea abies*; Pinus: *Pinus sylvestris;* Populus: *Populus* sp.; Prunus*: Prunus avium;* Pseudo: *Pseudotsuga menziesii*; Quercus: *Quercus* sp.; Tilia: *Tilia* sp. Mean values per stem, error bars show S.E., different characters indicate significant differences ($p< 0.001$).

In contrast to our expectations we found significantly more beetle species in conifer forests than in managed and unmanaged beech forests (Appendix II.b; Fig. II.B1). The comparisons of saproxylic species richness between deadwood logs of the same tree species in different regions revealed that logs in SCH hosted significant more species compared to exposed logs in ALB and HAI (Appendix II.A; Tab. II.A.2).

Deadwood logs of the main tree species contributed up to 56 % of the sampled regional species (Fig. II.3a-c). However, to cover up to 90 % of the observed regional saproxylic species a mixture of deadwood of nine tree species was necessary (Fig. II.3a-c). In the reverse order, significantly more tree species were necessary to cover up 50 % to 90 % of the regional species (t-test (t=6.005; p< 0.001; Fig. II.3d–f).

Multiplicative diversity partitioning revealed that alpha-diversity of saproxylic species of emerging from logs was lower than expected from a random distribution of individuals. The importance of beta-diversity differed among spatial scales. Increasing positive deviations from random distributions were observed among tree species within sites, among sites within forest types, among forest types within regions and among regions for saproxylic species richness. When abundant species were more strongly weighted (q=2), beta-diversity among sites within forest type was higher, but beta-diversity among regions lower than from a random distribution of individuals and species (Fig.II.4).

Nonmetric Multidimensional Scaling with following fitting of the factors showed that the hosted saproxylic beetle communities differed significantly between tree species, management types, and regions (Fig. II.5). Particularly, the saproxylic beetle community of Schorfheide-Chorin was dissimilar compared to the other regions. The difference between coniferous and deciduous trees was more pronounced than between forest management types (Fig. II.5).

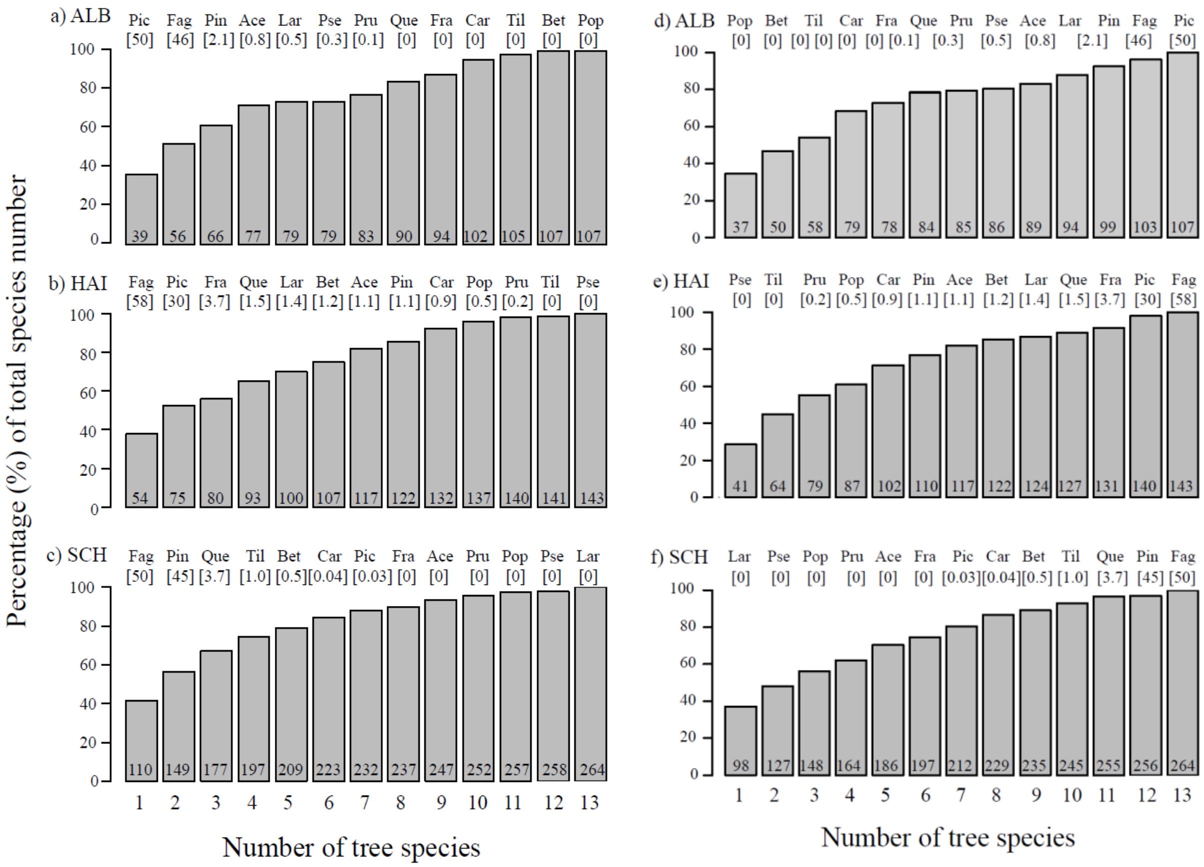


Fig. II.3: Percentage (%) of saproxylic beetle species number with increasing number of sampled tree species in the different study regions (ALB: Swabian Alb; HAI: Hainich-Dün; SCH: Schorfheide-Chorin). (a-c): tree species are ordered by (a - c) their commonness, and (d – f) their rareness within the study sites. Each new added tree species is given above the graphic (Ace: *Acer* sp.; Bet: *Betula pendula*; Car: *Carpinus betulus*; Fag: *Fagus sylvatica*; Fra: *Fraxinus excelsior*; Lar: *Larix decidua*; Pic: *Picea abies*; Pin: *Pinus sylvestris;* Pop: *Populus* sp.; Pru*: Prunus avium;* Pse: *Pseudotsuga menziesii*; Que: *Quercus* sp.; Til: *Tilia* sp.). Numbers in brackets give the proportion (%) of the total tree species composition of the added tree species of the study sites recorded by a forest inventory. Numbers within the bars give the total beetle species number sampled.

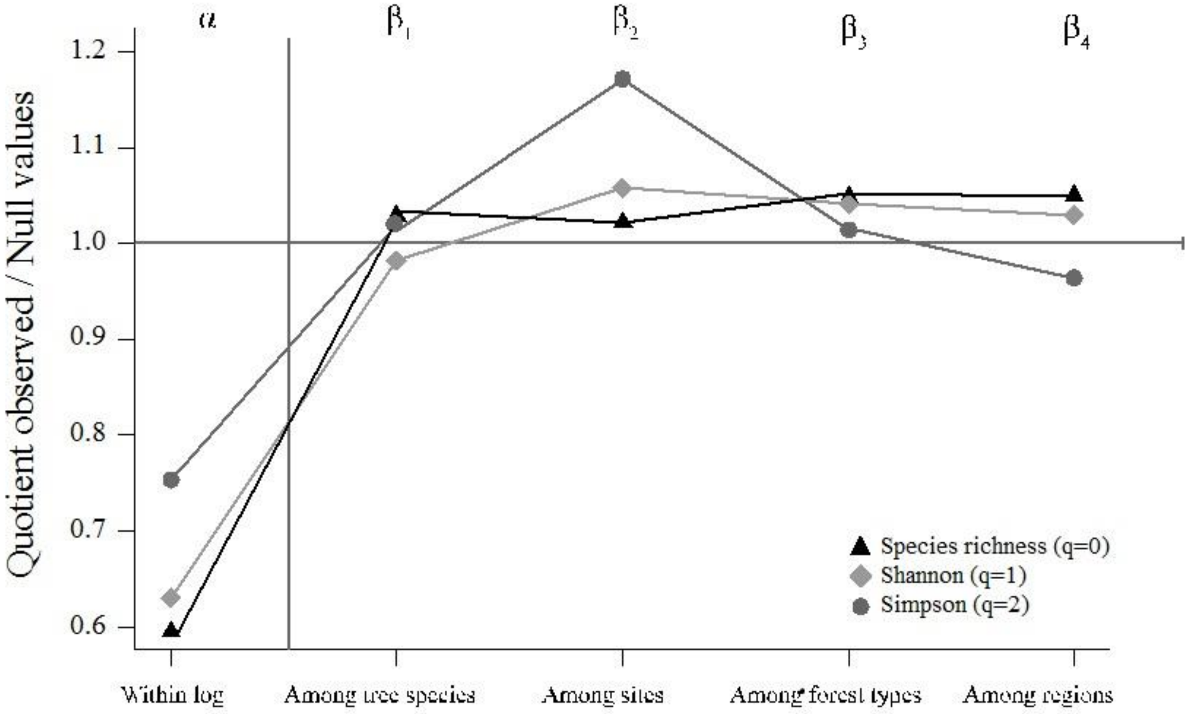


Fig. II.4: Multiplicative diversity partitioning (without sample weighting) of all saproxylic species sampled using Whittaker's multiplicative formula. The deviation from a Null distribution is illustrated by dividing observed values by the mean of Null values. Results of q statistics are shown for three q-values with increasing weighting of abundant species from 0 to 1 to 2. All differences were significant at the 0.05 level between diversity estimates and null estimates using 10,000 unrestricted individual-based randomizations, which is indicated by filled symbols.

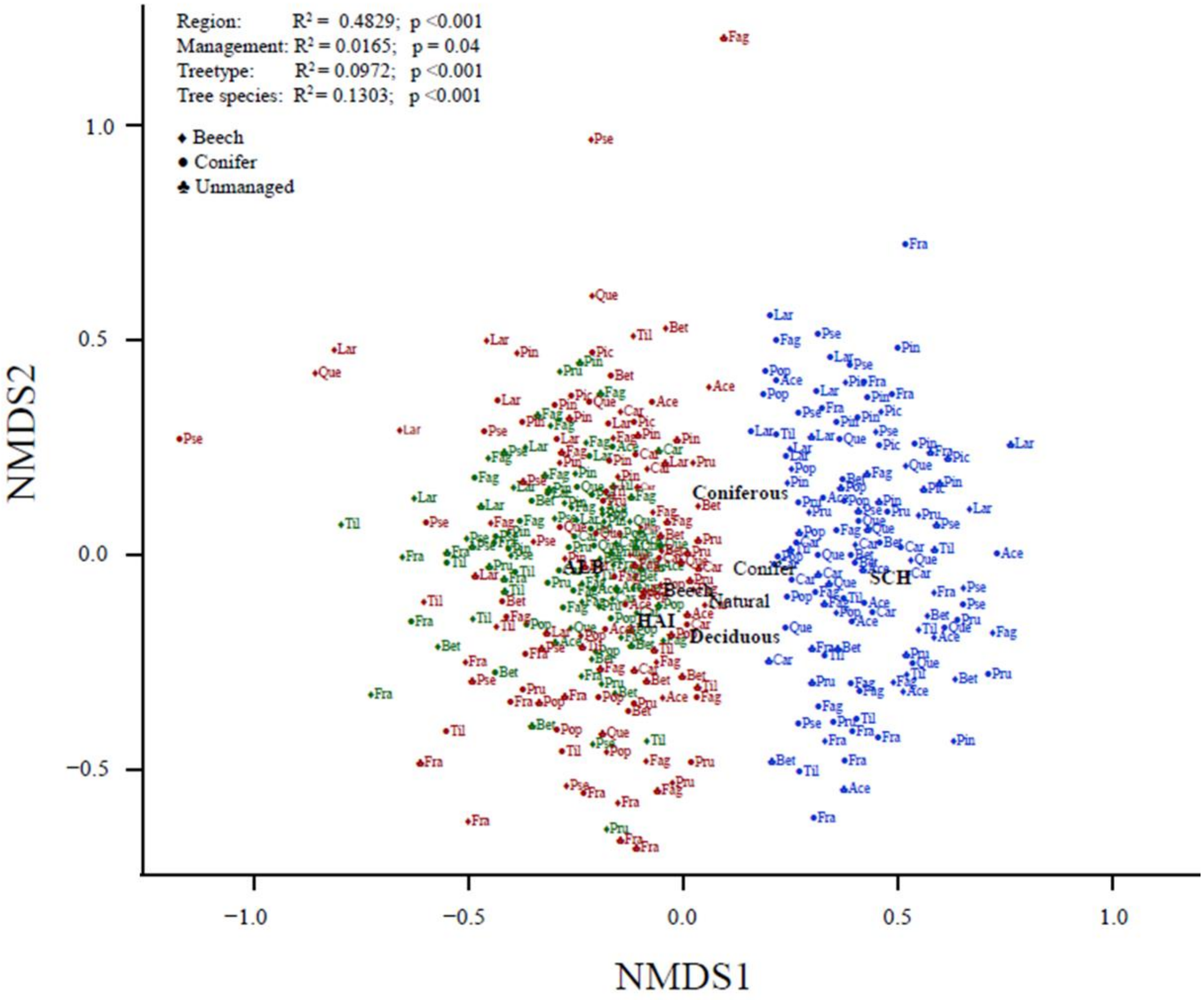


Fig. II.5: Non-metric multidimensional scaling (NMDS) and fitted environmental variables of saproxylic beetle communities sampled of deadwood logs of 13 tree species (Ace: *Acer* sp.; Bet: *Betula pendula*; Car: *Carpinus betulus*; Fag: *Fagus sylvatica*; Fra: *Fraxinus excelsior*; Lar: *Larix decidua*; Pic: *Picea abies*; Pin: *Pinus sylvestris;* Pop: *Populus* sp.; Pru*: Prunus avium;* Pse: *Pseudotsuga menziesii*; Que: *Quercus* sp.; Til: *Tilia* sp.) in three different forest management types and study regions, respectively. Stress value = 0.227. Different management types are indicated by different symbols and different study regions are indicated by different colors (Swabian Alb (ALB): green; Hainich-Dün (HAI): brown; Schorfheide-Chorin (SCH): blue).

Discussion

To disentangle the importance of tree species identity of deadwood, forest management, and regional context for the preservation of early successional saproxylic beetle diversity, we performed a large-scale experiment in central Europe. Deadwood of different tree species, management types and regions differed in saproxylic beetle species richness and contributed to overall diversity by high species turnover. Importantly, deadwood of the dominant tree species (beech, spruce, and pine) on the forest sites maintained only 50 % of local saproxylic beetle diversity. Our results emphasize the need for regionally adapted forest conservation schemes and deadwood management to maintain or even increase saproxylic beetle diversity on a national scale.

Tree species identity

Species richness of saproxylic beetles differed significantly between deadwoods of different tree species. Previous studies suggested that saproxylic diversity in well-decayed wood is only weakly influenced by tree species identity (Saint-Germain *et al.* 2006; Jonsell 2008; Thomas *et al.* 2009), whereas strong effects were found for fresh deadwood items (Lindhe & Lindelöw 2004; Lindbladh *et al.* 2007; Janssen *et al.* 2011; Lassauce *et al.* 2012). A successful colonisation and resource exploitation depends on the quality of the resource to meet the species specific requirements. Fresh deadwood of each tree species has its own specific structural and chemical properties, e.g. thickness and structure of the bark, moisture, lignin, and tannin content, as well as mineral inclusions of the wood, thus creating different habitat niches (Wagner *et al.* 2002). Similar to herbivore insects, early colonizing saproxylic beetles have to overcome these species specific properties (Cornwell *et al.* 2009; Fontaine *et al.* 2009). As proposed for herbivores feeding on plant tissue (Montoya *et al.* 2006), specialisation on deadwood of a particular tree genus might be more efficient for saproxylic beetles feeding on woody material than a generalistic diet.

Interestingly, deadwood of the most common tree species (beech, spruce, and pine) supported intermediate numbers of saproxylic beetle species and only about 50 % of the total species richness found per region. Depending on the region deadwood of hornbeam, maple and cherry supported most saproxylic beetle species. These findings could be explained by dilution effects of saproxylic beetles, due to locally higher availability of deadwood of the dominant tree species or of tree-specific differences in deadwood decay rates and resource quality. Deadwood of conifers is known to decay at slower rates and to host less diverse saproxylic communities than deciduous tree species (Thomas *et al.* 2009; Russell *et al.* 2014). Among the deciduous tree species the decay of hornbeam proceeds fast. The rapid decay and, consequently, the various microhabitats provided by hornbeam logs attracting simultaneously early successional and late successional beetle species might explain the overall high species richness of saproxylics.

Not only species richness but also saproxylic community composition varied between tree species. Spruce is known to shelter a dissimilar beetle composition compared to deciduous tree species (Saint-Germain *et al.* 2007; Jonsell 2008). Accordingly, we found dissimilar saproxylic beetle communities between coniferous and deciduous tree species. Therefore, to meet the demands of the diverse saproxylic beetle assemblages a wide variety of tree functional group (deciduous vs. coniferous) and tree species is crucial.

Management effects

Our results suggested that intensively managed conifer forests promote higher saproxylic beetle species richness than unmanaged beech forests. Possible reasons are higher amounts of fresh deadwood in managed spruce forests, the relatively short time scale of 10-30 years since the abandonment of management practices in beech forests, and different light regimes.

The meta-analysis of Paillet et al. (2010) showed that species richness in managed forests exceeds those in unmanaged forests within the first 20 years after forestry abandonment. Moreover, based on studies in Sweden it is assumed that it takes up to 270 to 300 years to re-establish the conditions of an old-growth forest (Hörnberg *et al.* 1998). Furthermore, forest with beech as dominant tree species show a U-shaped curve of size-dependent mortality with only few natural tree deaths in medium age (Holzwarth *et al.* 2013), resulting in dearth of natural occurring deadwood at this age. The investigated unmanaged beech forest sites are actually medium-aged, which might explain lower saproxylic species diversity due to lower amounts of deadwood. Due to commercial logging the local availability of fresh deadwood residues in managed forests is high. Furthermore, to maintaining saproxylic diversity temporal continuity of deadwood supply is of utmost importance (Vodka *et al.* 2008). In managed forests felled stems nearby the forest sites stored for transport provide suitable habitat for early colonizing saproxylic beetles till the next logging procedure will renew the deadwood supply.

A further possible explanation for differences in beetle diversity might be higher light permeability in coniferous stands than in beech forests as sun-exposure is one of the most important drivers of saproxylic beetle diversity (Hjältén *et al.* 2007; Johansson *et al.* 2007b; Vodka *et al.* 2008). Accordingly, Ranius and Jansson (2000) found that species richness was greatest in stands with large, free standing oak trees. Moreover, in some studies the majority of observed saproxylic beetles preferred sun-exposed logs, whereas only a small portion were exclusively found in shaded deadwood (Kaila *et al.* 1997; Jonsell *et al.* 1998; Horák *et al.* 2012; Koch Widerberg *et al.* 2012). Therefore, the higher insolation within conifer forests might provide early successional beetles preferring fresh, sun-exposed deadwood more suitable habitat conditions. Nevertheless, with ongoing succession we expect a shift of saproxylic diversity towards mature beech forests as many members of later successional beetle community prefer shaded, and advanced decayed deadwood (Hjältén *et al.* 2007; Jacobs *et al.* 2007; Thomas *et al.* 2009).

Regional effects

Regional differences in saproxylic beetle diversity could be related to management history, forest area, forest stand diversity, and biogeographical variation in species pools. We found highest species numbers and diversity of saproxylic beetles in Schorfheide-Chorin compared to the other regions. Our results contribute to the intermediate-disturbance hypothesis (Connell 1978), which postulates highest species diversity in systems with intermediate levels of disturbance due to a balanced frequency of different habitat types. Though forests in Schorfheide-Chorin developed after the last glacial event, large forest areas served as hunting areas, which allowed the development of diverse forest types; pine-oak forests, beech forests, oak-beech forests, as well as alder and birch forests with swamp patches (www.biodiversity-exploratories.de). Edge and spill-over effects between different forest types are known to enhance saproxylic diversity of early successional beetles due to good dispersal abilities (Okland et al. 1996; Wermelinger et al., 2007). Furthermore, understorey in these hunting forests was kept at low levels by herbivores, resulting in high levels of light permeability and sun-exposed forest patches. Adults of many saproxylic beetle species (e.g. long-horn beetles) depend not on woody material but on pollen or plant tissue provided by flowers. As flowering resources are more available in semi-open forests compared to closed forest sites these species benefit (Wermelinger *et al.* 2007).

Outlock

Importantly our study investigated the first steps of deadwood decay. According to Hjältén et al. (2007) and Saint-Germain et al. (2007), we expect that diversity patterns and community structure of saproxylic beetles will change with ongoing decay. Red-listed saproxylic beetles were sampled on the exposed fresh dead logs only at low species numbers. However, red-listed beetles are often specifically associated with well-decayed deadwood, e.g. *Osmoderma eremita* (Chiari *et al.* 2012). Therefore, we expect a peak in species richness of red-listed saproxylic beetles when the exposed deadwood logs will reach late successional stages.

Conclusion and conservation recommendations

To reduce or even stop the ongoing decline of the saproxylic beetle diversity in central European forests it is crucial to develop management schemes corresponding to the species-specific habitat and environmental requirements of saproxylic beetles. Our large-scale experiment underlines the importance of deadwood identity in terms of tree species for a high local and regional dissimilarity of the saproxylic beetle fauna. Therefore, short-term actions for saproxylic beetle conservation deadwood enrichment in terms of tree species variety would be very effective, although regional differences need to be considered. Long-term management should aim to convert monospecific forest stands into mixed forests with high deadwood diversity regarding tree species identity and decay stages to preserve diverse saproxylic beetle communities. However, further studies are required to document the long-term dynamics of saproxylic beetle diversity and to mitigate possible trade-offs between forest management and conservation objectives.

Appendix II.A

Tab. II.A.1: Number of deadwood logs and number and abundance of saproxylic beetle species and red listed saproxylic beetles in the study regions, the different management types, and tree species.

		Number of experimental logs	**Species Number/ abundance of saproxylic beetles**	**Species number/ abundance of saproxylic red listed beetles**
Region				
	Swabian Alb	199	107 / 9 821	5 / 57
	Hainich-Dün	222	143 / 15 614	8 / 55
	Schorfheide-Chorin	230	264 / 12 395	32 / 1 164
Management				
	Beech age class forest	227	208 / 13 318	15 / 320
	Conifer age class forest	252	257 / 17 757	24 / 837
	Unmanaged beech forest	172	183 / 6 755	17 / 112
Tree species				
	Acer sp.	50	127 / 8 491	8 / 341
	Betula pendula	51	135 / 2 644	5 / 57
	Fagus sylvatica	50	133 / 3 519	6 / 63
	Pseudotsuga menziesii	47	105 / 905	6 / 16
	Quercus sp.	52	136 / 3 893	10 / 32
	Fraxinus excelsior	51	113 / 675	3 / 8
	Picea abies	51	155 / 5 622	4 / 20
	Carpinus betulus	51	155 / 3 616	13 / 89
	Prunus avium	41	122 / 2 356	12 / 42
	Pinus sylvestris	52	131 / 1 135	8 / 37
	Larix decidua	52	127 / 1 154	7 / 60
	Tilia sp.	51	136 / 1 518	11 / 43
	Populus sp.	52	119 / 2 302	9 / 461

Tab. II.A.2: Pairwise comparisons of saproxylic species richness between deadwood logs of the same tree species in different regions (Acer: *Acer* sp.; Betula: *Betula pendula*; Carpinus: *Carpinus betulus*; Fagus: *Fagus sylvatica*; Fraxinus: *Fraxinus excelsior*; Larix: *Larix decidua*; Picea: *Picea abies*; Pinus: *Pinus sylvestris;* Populus: *Populus* sp.; Prunus*: Prunus avium;* Pseudotsuga: *Pseudotsuga menziesii*; Quercus: *Quercus* sp.; Tilia: *Tilia* sp.; ALB: Swabian Alb; HAI: Hainich-Dün; SHE: Schorfheide-Chorin). Significant differences (p< 0.05) are in bold.

	Estimate	**Std. Error**	**z-value**	**p-value**
HAI Acer - ALB Acer	1.179	1.500	0.786	0.5162
SHE Acer - ALB Acer	3.069	1.467	2.092	0.0629
SHE Acer - HAI Acer	1.890	1.457	1.297	**0.2635**
HAI Betula - ALB Betula	0.946	1.482	0.638	0.6107
SHE Betula - ALB Betula	8.826	1.467	6.016	**<0.0001**
SHE Betula - HAI Betula	7.880	1.439	5.477	**<0.0001**
HAI Carpinus - ALB Carpinus	-0.472	1.486	-0.318	0.8159
SHE Carpinus - ALB Carpinus	7.972	1.486	5.363	**<0.0001**
SHE Carpinus - HAI Carpinus	8.444	1.423	5.933	**<0.0001**
HAI Fagus - ALB Fagus	0.054	1.501	0.036	0.9740
SHE Fagus - ALB Fagus	5.891	1.486	3.963	**0.0003**
SHE Fagus - HAI Fagus	5.837	1.439	4.057	**0.0001**
HAI Fraxinus - ALB Fraxinus	-1.442	1.482	-0.973	0.4124
SHE Fraxinus - ALB Fraxinus	3.312	1.467	2.258	**0.0446**
SHE Fraxinus - HAI Fraxinus	4.755	1.439	3.304	**0.0025**
HAI Larix - ALB Larix	-0.306	1.467	-0.208	0.8852
SHE Larix - ALB Larix	5.417	1.467	3.692	**0.0007**
SHE Larix - HAI Larix	5.722	1.423	4.020	**0.0002**
HAI Picea - ALB Picea	1.610	1.482	1.086	0.3549
SHE Picea - ALB Picea	**6.667**	**1.467**	**4.544**	**<0.0001**
SHE Picea - HAI Picea	**5.056**	**1.439**	**3.514**	**0.0013**
HAI Pinus - ALB Pinus	-0.472	1.467	-0.322	0.8146
SHE Pinus - ALB Pinus	**4.250**	**1.467**	**2.897**	**0.0085**
SHE Pinus - HAI Pinus	**4.722**	**1.423**	**3.318**	**0.0024**
HAI Populus - ALB Populus	-0.145	1.467	-0.099	0.9398
SHE Populus - ALB Populus	7.410	1.467	5.051	**<0.0001**
SHE Populus - HAI Populus	7.556	1.423	5.309	**<0.0001**

Tab. II.A.2 continued

	Estimate	**Std. Error**	**z-value**	**p-value**
HAI Prunus - ALB Prunus	3.089	1.609	1.920	0.0910
SHE Prunus - ALB Prunus	7.713	1.629	4.736	**<0.0001**
SHE Prunus - HAI Prunus	4.625	1.547	2.989	**0.0065**
HAI Pseudotsuga - ALB Pseudotsuga	-0.801	1.563	-0.512	0.6947
SHE Pseudotsuga - ALB Pseudotsuga	4.510	1.533	2.943	**0.0075**
SHE Pseudotsuga - HAI Pseudotsuga	5.311	1.456	3.647	**0.0008**
HAI Quercus - ALB Quercus	-1.569	1.467	-1.070	0.3638
SHE Quercus - ALB Quercus	6.542	1.467	4.459	**<0.0001**
SHE Quercus - HAI Quercus	8.111	1.423	5.699	**<0.0001**
HAI Tilia - ALB Tilia	0.864	1.482	0.583	0.6454
SHE Tilia - ALB Tilia	8.153	1.467	5.557	**<0.0001**
SHE Tilia - HAI Tilia	7.289	1.439	5.065	**<0.0001**

Tab. II.A.3: List of all sampled beetle species and their host tree species.

	Acer sp.	*Betula pendula*	*Carpinus betulus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Larix decidua*	*Picea abies*	*Pinus sylvestris*	*Populus* sp.	*Prunus avium*	*Pseudotsuga menziesii*	*Quercus* sp.	*Tilia* sp.
Abraeus granulum	-	-	x	-	-	-	-	-	-	-	-	-	-
Abraeus perpusillus	x	x	x	x	x	-	x	-	x	x	x	-	x
Acalles camelus	x	x	x	-	x	x	-	x	-	-	-	-	-
Acalles hypocrita	x	x	x	x	-	-	-	-	x	x	-	-	-
Acritus minutus	-	x	-	-	-	-	-	-	x	-	-	x	-
Acrulia inflate	-	-	x	-	-	-	-	-	-	-	-	-	-
Aeletes atomarius	-	-	-	-	-	-	-	-	-	-	-	x	-
Agathidium nigripenne	x	-	x	x	x	x	x	x	x	x	-	x	x
Alosterna tabacicolor	-	-	-	-	-	x	-	-	-	-	-	-	-
Ampedus balteatus	x	x	x	x	x	-	-	x	x	x	x	x	x
Ampedus cinnabarinus	-	x	x	-	-	x	-	-	-	-	-	-	-
Ampedus elongatulus	-	x	x	-	-	-	x	-	-	-	-	-	-
Ampedus pomorum	x	x	x	x	x	x	-	x	x	x	x	x	x
Ampedus rufipennis	-	-	x	-	-	-	-	-	x	x	x	-	x
Ampedus sanguineus	-	x	x	-	x	x	x	x	-	x	x	x	x
Anaglyptus mysticus	-	-	-	x	-	-	-	-	-	-	-	-	-
Anaspis flava	-	x	-	-	-	x	-	-	-	-	-	x	-
Anaspis frontalis	x	-	-	-	-	x	-	-	x	-	-	-	-
Anaspis lurida	-	-	-	-	-	-	-	-	-	-	-	x	-
Anaspis regimbarti	-	x	-	-	-	-	-	-	-	-	-	-	-
Anaspis ruficollis	-	x	-	-	x	x	x	x	x	-	x	x	-
Anaspis rufilabris	-	x	x	-	-	-	x	x	x	-	-	x	x
Anaspis thoracica	-	x	-	-	x	x	-	x	x	-	-	x	x
Anisotoma castanea	-	-	-	-	-	x	-	-	-	-	-	-	-
Anisotoma humeralis	x	x	x	-	-	x	x	x	-	x	-	x	x

Anisotoma orbicularis	x	-	x	x	-	-	x	x	-	-	-	x	x
Anobium costatum	-	-	-	x	x	-	-	x	-	-	x	-	-
Anobium pertinax	-	x	-	x	-	x	x	x	-	x	x	x	-
Anomognathus cuspidatus	x	x	x	x	x	x	x	x	x	x	x	x	x
Anthribus albinus	x	-	x	x	-	-	-	-	-	-	-	-	x
Aplocnemus impressus	-	-	-	-	-	-	-	-	-	-	-	-	x
Aplocnemus nigricornis	-	-	-	-	-	-	x	-	-	-	-	-	-
Arpidiphorus orbiculatus	x	-	-	-	x	-	x	-	x	x	-	-	x
Atheta oblita	-	-	-	-	-	-	-	x	-	-	-	-	-
Atheta picipes	x	x	x	-	x	-	x	x	x	x	-	-	x
Atomaria bella	-	-	x	x	-	x	x	x	x	-	-	-	-
Atomaria ornata	-	-	-	-	-	-	-	-	x	-	-	-	-
Atomaria procerula	-	x	-	-	x	x	-	x	-	-	-	-	-
Atomaria turgida	-	-	-	-	-	-	x	-	-	-	-	-	-
Atrecus affinis	x	x	x	x	x	x	x	x	x	-	x	x	x
Batrisodes venustus	x	x	x	x	x	-	-	-	-	-	x	-	x
Bibloporus bicolor	x	x	x	x	x	x	x	x	x	x	x	x	x
Bibloporus mayeti	-	-	-	-	-	-	-	x	-	x	-	-	-
Bibloporus minutus	x	x	x	x	x	x	x	x	x	x	x	x	x
Bitoma crenata	x	x	x	x	-	x	x	-	x	x	x	x	x
Bolitochara lucida	x	-	x	-	-	-	-	-	-	-	-	-	-
Bolitochara obliqua	x	x	x	x	x	x	x	x	x	x	x	x	x
Bolitophagus reticulatus	-	-	-	-	-	-	-	-	-	-	-	-	x
Caenoscelis ferruginea	-	-	-	-	-	-	x	-	-	-	-	-	-
Cerylon fagi	x	x	x	x	x	x	x	x	x	x	x	x	x
Cerylon ferrugineum	x	x	x	x	x	x	x	x	x	x	x	x	x
Cerylon histeroides	x	x	x	x	x	x	x	x	x	x	x	x	x
Cetonia aurata	x	-	-	-	-	-	-	-	-	-	-	-	-
Choragus sheppardi	x	-	-	-	-	-	-	-	-	-	-	-	-
Cis boleti	x	x	x	x	-	x	x	x	x	x	-	x	x
Cis dentatus	-	-	x	-	-	-	-	-	-	-	-	-	-

Cis glabratus	-	-	-	-	-	-	x	x	x	-	-	-	-
Cis hispidus	x	x	-	x	-	-	x	x	-	x	-	x	-
Cis jacquemartii	-	-	-	-	-	-	-	-	-	-	-	-	x
Cis micans	-	-	-	-	-	-	-	-	-	x	-	-	-
Cis nitidus	-	-	-	-	-	-	-	-	-	-	-	x	-
Cis punctulatus	-	x	-	-	-	-	x	-	-	-	-	-	-
Cis rugulosus	-	-	x	-	-	-	-	-	-	x	-	-	-
Cis setiger	-	-	-	-	-	-	x	-	-	-	-	-	-
Corticaria abietorum	x	x	x	x	x	x	x	x	x	x	x	x	x
Corticaria inconspicua	x	-	-	-	-	-	-	-	-	-	-	-	-
Corticaria linearis	x	-	-	-	x	x	-	-	-	x	x	x	x
Corticaria longicollis	-	-	-	-	-	-	x	x	-	-	-	-	-
Corticaria pineti	-	-	x	-	-	-	-	-	-	-	-	-	-
Corticaria serrata	-	-	-	x	-	-	-	-	-	-	-	-	-
Corticarina lambiana	-	-	-	-	-	-	-	-	-	-	-	x	-
Corticarina obfuscata	x	x	x	x	x	x	x	x	x	x	x	x	x
Corticeus unicolor	x	x	x	x	-	x	x	x	x	x	x	x	x
Corymbia rubra	-	-	-	x	x	x	x	x	-	-	x	-	-
Corymbia scutellata	-	-	x	-	-	-	-	-	-	-	-	-	-
Coryphium angusticolle	-	-	x	x	-	x	x	x	-	-	-	x	x
Cryphalus abietis	-	-	-	-	-	-	x	-	-	-	-	-	-
Cryptolestes duplicatus	-	-	-	-	-	-	x	-	-	-	-	x	-
Cryptophagus dorsalis	-	x	x	-	x	x	x	x	x	x	x	x	x
Cryptophagus labilis	-	-	-	-	-	-	-	-	-	-	-	-	x
Cryptophagus micaceus	-	-	x	-	-	-	-	-	-	-	-	-	-
Crypturgus cinereus	-	x	-	-	x	-	x	x	x	x	x	x	x
Crypturgus hispidulus	x	x	x	x	x	x	xx	x	x	-	x	x	x
Crypturgus pusillus	-	-	-	-	-	-	x	-	-	-	-	-	-
Cychramus variegatus	-	-	-	-	x	-	-	-	-	-	-	-	x
Cyphea curtula	-	-	-	-	x	-	-	-	-	-	-	-	x
Dacne bipustulata	-	-	-	x	-	-	-	x	-	x	-	-	-

Dadobia immersa	x	x	x	x	x	x	x	x	x	x	x	x	x
Dasytes aeratus	-	x	x	-	-	x	-	-	-	-	-	x	x
Dasytes plumbeus	-	-	-	-	-	-	-	x	-	-	-	-	-
Denticollis linearis	x	x	-	-	-	x	-	-	x	x	-	x	x
Denticollis rubens	-	-	x	-	-	-	-	-	-	x	-	-	-
Dexiogya corticina	-	x	-	x	-	-	-	-	-	-	x	-	-
Dinaraea aequata	x	x	x	x	-	x	x	x	x	x	x	x	x
Dinaraea linearis	-	-	x	-	-	x	-	x	-	-	-	-	-
Diplocoelus fagi	-	x	x	x	-	x	-	-	-	-	-	-	x
Dissoleucas niveirostris	x	-	-	-	-	-	-	-	-	-	-	-	-
Dorcus parallelipipedus	-	x	-	-	-	x	-	-	-	-	-	-	-
Dryocoetes autographus	-	-	x	-	x	x	x	x	x	x	x	x	-
Dryocoetes villosus	-	-	-	-	-	-	x	-	x	-	-	x	x
Endomychus coccineus	x	x	x	x	-	x	-	x	x	x	x	-	x
Enicmus atriceps	-	x	-	-	-	x	-	x	-	-	-	-	x
Enicmus brevicornis	-	-	x	x	-	-	-	-	-	-	-	-	x
Enicmus fungicola	-	-	x	-	-	x	-	-	-	x	-	x	-
Enicmus planipennis	-	x	-	-	-	x	-	-	x	-	-	-	-
Enicmus testaceus	-	-	-	-	-	x	x	x	x	x	-	-	-
Ennearthron cornutum	-	x	-	x	-	-	-	-	-	-	-	x	x
Epuraea limbata	-	-	-	-	-	-	-	-	-	-	-	x	x
Epuraea longula	-	-	-	x	-	-	-	-	-	-	-	-	-
Epuraea marseuli	-	-	-	-	-	-	-	-	-	-	x	-	-
Epuraea neglecta	-	-	x	-	-	-	-	-	-	-	-	-	-
Epuraea pygmaea	-	-	x	-	-	-	-	-	-	-	-	x	-
Epuraea variegata	-	-	-	x	-	-	-	-	-	-	-	-	-
Ernobius mollis	x	x	-	-	-	x	x	-	-	x	-	-	-
Ernobius nigrinus	-	-	-	-	x	-	-	-	-	-	-	-	x
Ernoporicus fagi	-	x	x	x	x	x	x	x	-	-	-	x	x
Euplectus brunneus	x	x	x	-	-	-	-	x	x	-	-	-	-
Euplectus decipiens	-	-	x	-	x	x	x	x	x	x	x	x	x

Euplectus fauveli	x	x	x	x	x	x	x	x	x	x	x	x	x
Euplectus infirmus	-	-	x	x	-	x	x	x	-	-	-	-	-
Euplectus karsteni	x	x	x	-	x	x	x	x	x	-	x	x	x
Euplectus kirbyi	x	x	x	x	x	x	x	x	x	x	x	x	x
Euplectus nanus	x	x	x	x	x	x	x	x	x	x	x	x	x
Euplectus piceus	-	-	x	x	x	x	x	x	x	x	x	x	x
Euplectus punctatus	x	x	x	x	x	x	x	x	x	x	x	x	x
Euplectus tholini	-	x	-	x	-	-	x	-	-	-	-	-	-
Euryusa castanoptera	-	x	x	-	-	-	-	x	x	x	x	x	-
Gabrius splendidulus	x	x	x	x	x	x	x	x	x	x	x	x	x
Glischrochilus quadripunctatus	-	-	-	-	x	x	-	x	-	x	-	-	x
Globicornis corticalis	-	-	-	-	-	-	-	-	-	-	-	-	x
Gyrophaena boleti	-	-	-	x	-	x	-	-	-	-	-	-	-
Gyrophaena minima	-	-	x	x	x	-	-	-	-	-	-	-	-
Hedobia imperialis	x	-	x	-	-	-	x	-	-	-	-	x	-
Hololepta plana	-	-	-	-	-	-	-	-	x	-	-	-	-
Homalota plana	-	-	x	-	-	-	-	-	x	x	-	-	x
Hylastes attenuatus	-	-	-	-	-	-	x	x	-	-	-	-	-
Hylecoetus dermestoides	x	x	x	-	-	x	x	x	x	x	x	x	x
Hylesinus crenatus	x	-	-	-	x	-	-	-	-	-	-	-	-
Hylis cariniceps	-	-	-	-	-	x	-	-	-	-	-	-	x
Hylis foveicollis	-	-	x	x	-	-	-	x	-	x	x	-	-
Hylis olexai	-	-	x	-	-	-	-	-	-	-	-	-	-
Hylobius abietis	-	-	-	-	x	-	-	-	-	-	-	-	-
Hylurgops palliatus	x	-	x	-	x	x	x	x	x	-	x	x	x
Hypnogyra glabra	-	-	-	-	-	x	-	-	-	-	-	-	-
Ischnoglossa prolixa	-	-	-	-	-	x	-	-	-	-	-	-	-
Ischnomera cyanea	-	-	-	-	-	-	-	-	-	-	-	x	-
Ischnomera sanguinicollis	-	-	-	-	-	-	-	-	x	-	-	-	-
Laemophloeus monilis	-	-	-	-	-	-	-	-	-	-	-	-	x

Latridius consimilis	x	x	x	-	x	x	x	x	-	x	x	x	x
Latridius hirtus	-	-	-	-	x	-	x	x	-	x	-	x	x
Leiopus nebulosus	x	-	x	-	-	-	-	-	-	-	-	-	x
Leperisinus fraxini	-	-	-	-	x	-	-	-	-	-	-	-	-
Leptoplectus spinolae	-	-	-	-	-	-	-	-	-	x	-	-	x
Leptura quadrifasciata	-	-	x	-	-	-	x	-	-	-	-	-	-
Leptusa fumida	x	x	x	x	x	x	x	x	x	x	x	-	x
Leptusa pulchella	x	x	x	x	x	x	x	x	x	x	x	x	x
Litargus connexus	x	-	x	x	x	-	-	-	x	-	-	-	-
Malachius bipustulatus	-	x	-	-	-	-	-	-	-	-	-	-	-
Malthinus facialis	-	-	-	x	-	-	-	-	-	-	-	-	-
Malthinus punctatus	-	x	x	x	-	x	-	-	-	-	-	-	x
Malthodes crassicornis	-	-	-	-	-	-	x	-	x	x	-	x	-
Malthodes guttifer	x	-	-	-	-	-	-	-	-	-	-	-	x
Malthodes marginatus	-	-	-	-	-	x	-	-	-	-	-	-	-
Malthodes pumilus	x	-	-	x	x	x	x	x	x	x	x	-	x
Malthodes spathifer	-	x	x	-	-	-	-	-	-	-	-	-	-
Megatoma undata	-	-	x	x	x	-	-	x	x	-	x	-	-
Melandrya barbata	x	-	x	-	-	-	-	-	-	-	-	-	-
Melandrya caraboides	-	-	-	-	-	-	-	-	-	x	-	-	-
Melanotus castanipes	x	x	x	x	-	x	x	x	x	x	x	x	x
Melanotus rufipes	x	x	x	x	-	x	x	x	x	x	x	x	x
Melasis buprestoides	-	x	x	x	-	-	-	-	-	-	-	x	-
Mesocoelopus niger	-	-	x	-	-	-	-	-	-	-	-	-	-
Micrambe abietis	x	x	x	x	x	x	x	x	x	x	x	x	x
Micridium halidaii	-	-	x	x	-	-	x	-	-	-	-	-	-
Microscydmus minimus	x	x	x	x	x	x	x	x	x	x	x	x	x
Mycetina cruciata	x	x	x	x	-	-	-	x	-	-	-	-	x
Mycetophagus atomarius	-	-	x	x	-	-	-	-	-	-	-	-	-
Mycetophagus fulvicollis	-	-	-	-	-	-	-	-	x	x	-	-	-
Mycetophagus	-	x	-	x	-	-	-	-	-	-	-	-	-

quadripustulatus													
Nemadus colonoides	-	-	-	-	-	-	-	-	x	-	-	-	-
Nemosoma elongatum	x	-	-	-	-	-	-	-	x	x	-	-	-
Neuraphes carinatus	-	x	-	-	-	x	-	x	x	x	x	x	-
Neuraphes plicicollis	-	-	-	-	-	-	-	x	-	-	-	-	-
Nosodendron fasciculare	-	-	-	-	-	-	-	-	-	-	-	x	-
Nudobius lentus	x	-	x	x	-	x	x	x	x	x	x	x	-
Obrium brunneum	-	-	-	x	-	-	-	-	-	-	-	-	-
Octotemnus glabriculus	x	x	x	x	x	-	-	x	-	x	x	x	x
Oligota granaria	-	-	-	-	-	-	-	-	-	x	-	-	-
Opilo mollis	-	x	-	-	-	x	-	-	-	-	-	-	-
Orchesia micans	-	-	x	-	-	-	-	-	-	-	x	-	-
Orchesia minor	x	-	-	-	-	-	x	-	-	-	-	-	-
Orchesia undulata	x	-	x	x	x	-	-	-	-	x	-	x	-
Orthocis alni	-	-	x	x	x	-	x	-	x	x	x	x	-
Orthocis festivus	-	-	x	-	-	x	-	x	-	x	x	x	-
Orthoperus atomus	-	x	x	x	x	x	x	x	x	x	-	x	x
Orthoperus mundus	x	x	x	x	x	-	x	x	x	x	x	x	x
Orthoperus nigrescens	-	-	x	-	-	-	-	-	-	-	-	-	-
Orthotomicus laricis	-	-	-	-	-	-	x	-	-	-	-	-	-
Oxypoda recondita	x	-	-	-	-	-	x	-	x	x	x	-	x
Pachytodes cerambyciformis	-	-	-	x	-	-	-	-	-	-	-	-	-
Paromalus flavicornis	x	x	x	x	x	x	x	x	x	-	x	x	x
Paromalus parallelepipedus	-	x	-	-	-	x	x	x	-	-	-	x	-
Pediacus depressus	x	-	-	-	-	-	-	-	-	-	x	-	-
Phloeocharis subtilissima	x	x	x	x	x	x	x	x	x	x	x	x	x
Phloeonomus punctipennis	x	x	x	x	x	x	x	x	x	x	x	x	x
Phloeonomus pusillus	-	-	-	-	x	-	x	x	-	-	-	-	x
Phloeopora corticalis	x	x	x	x	x	x	x	-	x	x	x	x	x

Phloeopora testacea	x	x	x	x	-	-	x	x	-	-	-	-	x
Phloeostiba lapponicus	-	x	-	-	-	-	-	-	-	-	-	-	-
Phloeostiba planus	-	-	-	-	x	-	-	-	-	-	-	-	-
Phyllodrepa ioptera	-	-	x	-	x	-	-	-	-	-	-	-	-
Phyllodrepa linearis	-	x	x	-	x	x	x	x	-	-	x	-	x
Phyllodrepa nigra	-	-	-	x	-	-	x	-	-	x	-	x	-
Phyllodrepoidea crenata	-	-	x	-	-	-	-	-	-	-	-	-	-
Pityophagus ferrugineus	-	-	-	-	-	-	x	-	-	-	-	-	-
Pityophthorus lichtensteini	-	-	-	x	-	-	-	-	-	-	-	-	-
Pityophthorus pityographus	-	-	-	-	-	x	-	-	x	-	-	-	-
Pityophthorus pubescens	-	-	-	-	x	-	-	-	-	-	-	-	-
Placonotus testaceus	-	-	x	x	-	-	-	-	-	-	-	x	-
Placusa atrata	-	x	-	x	-	-	-	-	x	-	-	-	-
Placusa tachyporoides	-	-	-	-	-	x	-	-	-	-	-	-	-
Platycerus caraboides	-	x	-	-	-	x	-	-	-	-	-	-	-
Platydema violaceum	-	-	-	-	-	-	x	-	-	-	-	-	-
Platyrhinus resinosus	-	-	-	x	-	-	-	-	-	-	-	-	x
Platysoma compressum	-	-	x	-	-	-	x	-	-	-	-	-	x
Platysoma lineare	-	-	-	-	-	x	-	-	-	-	-	-	-
Plectophloeus fischeri	x	x	x	x	x	x	x	x	x	x	x	x	x
Plectophloeus nitidus	x	x	x	x	x	x	x	x	x	x	-	x	x
Plectophloeus nubigena	x	x	x	x	x	x	x	x	x	x	x	x	x
Plegaderus caesus	-	x	-	-	-	-	x	-	-	-	-	-	-
Plegaderus dissectus	x	x	x	x	x	x	x	x	x	x	x	x	x
Plegaderus vulneratus	-	-	-	-	x	-	-	-	-	-	-	-	-
Pogonocherus fasciculatus	-	-	-	-	x	-	x	x	x	x	-	x	-
Pogonocherus hispidulus	-	-	-	-	-	-	-	-	-	-	-	-	x
Prionocyphon serricornis	x	-	-	x	-	-	-	-	-	-	-	x	x
Prionychus ater	-	-	-	-	-	-	-	-	-	-	-	-	x
Ptenidium gressneri	-	-	-	-	-	-	-	-	x	-	-	-	-
Pteryx suturalis	x	x	x	x	x	x	x	x	x	x	x	x	x

Ptilinus pectinicornis	x	x	x	x	x	x	x	x	x	x	x	x	x
Ptinella aptera	x	x	x	x	-	x	x	x	x	x	x	x	x
Ptinella limbata	x	-	x	x	x	x	x	x	x	-	-	-	-
Ptinella tenella	x	x	x	x	x	x	x	x	x	x	x	x	x
Pyrochroa coccinea	x	x	x	x	-	-	-	-	x	-	-	x	x
Pyrrhidium sanguineum	-	-	-	-	-	-	-	-	-	-	-	x	-
Pytho depressus	-	-	-	-	-	-	x	x	x	-	x	-	-
Quedius maurus	x	-	-	-	-	-	-	x	-	-	-	-	-
Quedius scitus	x	x	x	x	x	-	x	x	x	x	x	x	x
Quedius xanthopus	x	x	x	x	x	x	x	x	x	x	x	x	-
Rabocerus foveolatus	-	-	-	-	-	-	x	-	-	-	-	x	-
Rhagium bifasciatum	-	-	-	-	-	-	-	x	-	x	-	-	-
Rhagium inquisitor	-	-	-	-	-	x	x	x	-	-	x	-	-
Rhagium mordax	x	x	x	x	x	-	-	-	x	x	x	x	x
Rhizophagus bipustulatus	x	x	x	x	x	x	x	x	x	x	x	x	x
Rhizophagus cribratus	x	-	-	-	-	-	-	-	-	-	-	-	-
Rhizophagus depressus	x	x	x	x	x	x	x	x	x	x	x	x	x
Rhizophagus dispar	x	x	x	x	x	x	x	x	x	x	x	x	x
Rhizophagus ferrugineus	x	-	-	-	-	-	-	-	-	-	-	-	-
Rhizophagus nitidulus	x	x	x	x	-	-	x	x	x	x	x	x	x
Rhizophagus parvulus	x	x	x	x	x	x	-	x	x	-	-	x	x
Rhizophagus perforatus	-	x	-	-	-	-	-	-	-	x	-	-	-
Rhizophagus picipes	-	x	-	-	-	-	-	-	-	-	-	-	-
Rhyncolus ater	x	x	-	-	x	x	x	x	x	-	x	x	-
Rhyncolus elongatus	x	-	-	-	-	x	-	x	-	-	-	-	-
Rhyncolus sculpturatus	-	-	x	x	-	-	-	-	-	-	-	-	-
Salpingus aeratus	-	-	-	-	x	-	-	-	-	-	-	-	-
Salpinus planirostris	x	x	-	x	x	-	-	-	-	-	-	x	-
Salpingus ruficollis	-	x	x	x	x	x	-	-	x	-	x	x	x
Saperda scalaris	-	-	x	-	-	-	-	-	-	-	-	-	-
Saulcyella schmidtii	-	-	-	-	-	-	-	-	-	x	-	-	-

Scaphidium quadrimaculatum	-	-	-	x	-	-	-	-	-	-	x	-	-
Scaphisoma agaricinum	x	x	x	x	x	x	x	x	-	x	x	x	x
Schizotus pectinicornis	x	-	x	-	x	-	-	-	-	x	-	x	-
Scolytus intricatus	-	-	-	x	-	-	-	-	-	-	-	-	-
Scraptia fuscula	-	-	x	-	-	-	-	-	-	-	-	-	-
Sepedophilus testaceus	x	x	x	x	x	x	x	-	x	x	x	x	x
Serropalpus barbatus	-	-	-	-	-	x	x	-	-	-	-	-	-
Siagonium quadricorne	-	-	-	-	-	-	-	-	x	-	-	-	-
Silvanoprus fagi	-	-	-	-	-	-	-	-	-	-	-	x	-
Silvanus bidentatus	-	-	-	-	-	-	-	x	-	-	-	x	x
Silvanus unidentatus	x	x	x	-	-	-	x	-	x	x	x	x	x
Sinodendron cylindricum	x	x	x	x	x	x	-	x	x	x	-	x	x
Sphaeriestes castaneus	x	-	-	-	-	-	-	-	-	-	-	-	-
Sphindus dubius	-	x	x	-	-	x	-	-	-	x	x	x	x
Stenagostus rhombeus	-	x	-	-	-	-	-	-	-	-	-	x	x
Stenichnus bicolor	x	x	x	x	x	x	x	x	x	x	x	x	x
Stenichnus collaris	x	x	x	x	x	x	x	x	x	x	x	x	x
Stenichnus godarti	x	x	x	x	x	x	x	x	x	x	x	x	x
Stenostola dubia	-	-	-	-	-	-	-	-	-	-	-	-	x
Stephostethus alternans	-	x	-	x	-	x	x	x	x	-	-	-	-
Stephostethus rugicollis	x	-	-	x	x	-	-	-	-	-	-	-	-
Stereocorynes truncorum	-	-	-	-	-	-	x	-	-	x	-	-	x
Sulcacis affinis	x	-	-	x	-	x	-	-	-	x	-	-	-
Sulcacis fronticornis	x	-	-	-	-	-	-	x	-	x	x	-	-
Synchita humeralis	-	-	-	x	-	-	-	-	-	-	-	-	-
Tachyta nana	-	x	x	-	-	-	-	-	-	-	-	x	-
Tachyusida gracilis	-	-	-	-	-	-	-	-	-	-	-	x	-
Taphrorychus bicolor	x	x	x	x	x	x	x	x	-	x	x	x	x
Thanasimus formicarius	-	-	-	x	x	-	x	x	-	-	-	-	x
Tillus elongatus	-	x	x	-	-	-	-	-	-	-	-	-	-

Tomoxia bucephala	x	x	x	x	-	x	-	-	-	x	-	-	-
Trachodes hispidus	-	x	x	x	x	x	x	-	x	x	x	x	x
Triochonyx sulcicollis	-	-	-	-	-	-	-	-	-	-	x	-	-
Triphyllus bicolor	x	-	x	-	-	-	-	x	-	-	-	x	-
Triplax aenea	x	x	-	-	-	-	-	-	-	-	-	-	-
Triplax russica	-	-	-	x	-	-	-	-	-	-	-	-	-
Tritoma bipustulata	x	-	-	x	-	-	-	-	-	-	-	-	-
Tropideres albirostris	-	-	-	x	-	-	-	-	-	-	-	-	-
Tyrus mucronatus	x	x	x	x	x	x	-	-	x	x	-	x	-
Uleiota planata	x	x	x	x	x	x	-	x	x	x	x	x	x
Uloma culinaris	-	-	-	-	-	-	-	-	-	x	-	-	-
Variimorda fasciata	-	-	x	-	-	-	-	-	-	x	-	-	-
Vincenzellus ruficollis	x	-	x	x	x	x	x	x	x	x	x	x	x
Xestobium plumbeum	-	-	-	-	-	-	-	x	-	-	x	x	-
Xyleborus dispar	-	x	-	-	x	-	x	x	-	-	x	x	x
Xyleborus germanus	x	x	x	x	x	x	x	x	x	x	x	x	x
Xyleborus monographus	x	x	-	-	x	x	x	-	-	-	-	x	x
Xyleborus peregrinus	x	-	-	-	-	-	-	-	-	-	-	-	-
Xyleborus saxeseni	x	x	x	x	x	-	x	x	x	x	x	x	x
Xylita laevigata	x	-	-	-	-	x	x	x	-	-	-	-	-
Xylostiba bosnicus	-	-	-	-	-	-	-	x	-	-	-	-	-
Xylostiba monilicornis	x	-	x	x	x	-	-	-	x	x	x	x	-
Xyloterus domesticus	x	x	x	x	x	x	x	x	x	x	x	x	x
Xyloterus lineatus	-	x	x	x	-	-	-	-	-	-	-	-	x
Xyloterus signatus	x	x	x	x	x	x	-	-	x	-	x	x	x

Appendix II.B

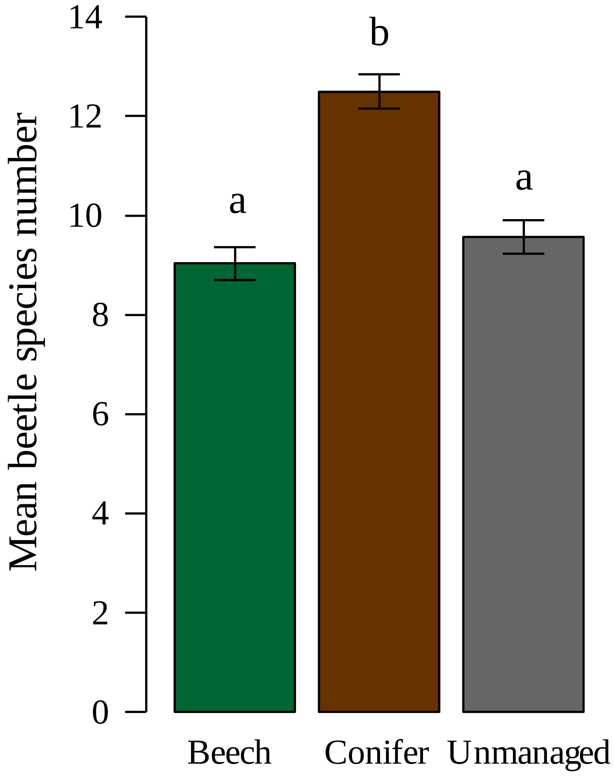


Fig. II.B.1: Comparison of species richness (mean values per management type, error bars show S.E.) of saproxylic beetles and between differently managed forest types (Conifer: conifer forests, Beech: managed beech forests; Unmanaged: unmanaged beech forests). Different characters indicate significant differences. Mean values per management type, error bars show S.E.

CHAPTER III: SPECIALISATION OF SAPROXYLIC BEETLE INTERACTION NETWORKS DEPENDS ON TROPHIC LEVEL

Abstract

The specialisation degree of ecological networks has been used to evaluate functional consequences of biodiversity loss. Furthermore, it has been shown that the tolerance of ecological communities to anthropogenic disturbance depends on functional redundancy of interacting partners and network topology. These studies focussed on mutualistic plant-pollinator or antagonistic plant-herbivore interaction networks, but related studies of decomposer networks are noticeably rare. Here, we investigated the interactions of saproxylic beetles with 651 experimentally exposed fresh deadwood logs of 13 tree species in 27 forest sites in managed conifer and managed and unmanaged beech forests in three regions across Germany. We assumed that intensive forest management negatively affects the specialisation degree of saproxylic beetle sub-guilds of different trophic levels. For the 392 sampled saproxylic beetle species 37,243 interactions with the 13 tree species were recorded. Overall, specialisation of saproxylic beetle interaction networks was remarkably high. However, specialisation decreased from xylophagous through mycetophagous to predatory saproxylic beetle species. Network specialisation was not affected by forest management and this pattern was consistent for trophic saproxylic beetle sub-guilds in all regions. We conclude that due to the overall high degree of specialisation, interaction networks of primary saproxylic beetles are highly susceptible to species loss of both tree species and beetle species.

Keywords

Decomposition; ecosystem function; guilds; forest management; emergence traps; deadwood

Introduction

Analyses of interaction networks are a valuable tool in community ecology to quantify and compare complex plant-animal interactions, and to predict the consequences of species loss for ecosystem stability and functioning (McCann 2000; Loreau *et al.* 2001; Montoya *et al.* 2006; Bascompte & Jordano 2007; Blüthgen *et al.* 2007; Weiner *et al.* 2014). In ecological networks, specialists establish only few interactions to a restricted group of species, whereas generalists interact randomly with many species (Guimarães *et al.* 2006; Vacher *et al.* 2008). Due to the narrow ecological niche, especially habitat and diet specialists are confronted with an increased extinction risk under anthropogenic environmental change (Biesmeijer *et al.* 2006; Devictor *et al.* 2008; Colles *et al.* 2009; Clavel *et al.* 2011; Burkle *et al.* 2013). Therefore, generalists are typically expected to dominate in anthropogenically manipulated landscapes as they may benefit from environmental changes due to their ability to perform well in heterogeneous environments (Devictor *et al.* 2008).

European forest ecosystems have been disturbed and fragmented by humans since the resettlement of forests after the last glaciation, leaving less than 1% as natural forests (Paillet *et al.* 2010). Furthermore, intensified forest management practices due to technological advances and the increasing demand for bioenergy production have led to severe species loss in forest ecosystems during the last century (Niemela 1997; Bengtsson *et al.* 2000; Schmiegelow & Mönkkönen 2002; Schröter *et al.* 2005; Ciesla 2011). Particularly the species-rich group of deadwood-dependent species has been negatively affected by intensive management due to the loss of essential deadwood resources (Okland *et al.* 1996; Martikainen *et al.* 2000; Siitonen 2001; Grove 2002b; Brunet & Isacsson 2009; Gossner *et al.* 2013).

Species diversity is considered as key to ecosystem functioning (Scherer-Lorenzen *et al.* 2005). The loss of species is expected to have severe consequences for the perpetuation of ecosystem services (Loreau *et al.* 2001; Foley *et al.* 2005; Tylianakis *et al.* 2007; Laliberté & Tylianakis 2010). Based on their crucial initial role in the decomposition of woody material, saproxylic species play a key role in preserving the soil nutrient pool by dislocating nutrients from woody detritus and dispersing fungal spores (Speight 1989, Pyle and Brown 1999 and references herein, Spence 2001, Vanderwel et al. 2006, Quinto et al. 2012). Consequently, saproxylic species loss might slow down the decomposition process and negatively affect nutrient cycling (Tilman 1997, Jacobs et al. 2007). However, simply counting species and thereby disregarding species interactions of beetles and their dead host trees could lead to wrong assumptions concerning the robustness and functioning of forest ecosystems (McCann 2000; Hillebrand & Matthiessen 2009; Morris 2010).

From a functional perspective, saproxylic beetles can be subdivided in guilds (groups of functionally similar species), which either mirror the trophic level (xylophages, mycetophages, and predators). Due to functional redundancy, species rich guilds provide ecosystem stability and determine the performance of ecosystem processes (Root 1967; Hawkins & MacMahon 1989; Naeem & Li 1997; Tilman 1997; Trindade-Filho *et al.* 2012). Furthermore, in ecological networks high functional redundancy is often accompanied by generalistic behaviour of the participating species (Blüthgen & Klein 2011). However, knowledge about properties of wood-decomposer interaction networks is scarce, though wood-dependent sub-networks seem to contain more generalists than insect-dependent sub-networks (Quinto *et al.* 2012). Moreover, effects of forest management on saproxylic interaction networks are little investigated (Miranda *et al.* 2013).

In this study, we analysed saproxylic beetle interaction networks with their dead host trees in temperate forest habitats comprising three forest management strategies in a large-scale experimental approach. We recorded the colonisation of 688 exposed deadwood logs of 13 tree species by saproxylic beetles and assessed network specialisation in a total of 27 sites across three regions.

Due to the overall high species richness of saproxylic beetles (Köhler 1996, 2000) and thus expected high functional redundancy we predict (1) a general low network specialisation of saproxylic beetle interaction networks in temperate ecosystems. (2) As higher specialised species are more vulnerable to habitat loss, network specialisation should decrease with the intensification of forest management. Primary colonizers have to overcome tree species qualities, as wood produced by different tree species varies substantially in chemical, micro- and macro-morphological characteristics (Poelman *et al.* 2008; Cornwell *et al.* 2009). Therefore, we predict that (3) wood-dependent sub-networks of early successional xylophages are more specialised than fungi-dependent and insect-dependent sub-networks of higher trophic levels.

Material and Methods

Biodiversity Exploratories

The research was performed in the framework of the Biodiversity Exploratories, a large-scale and long-term project on the effects of land use on biodiversity and ecosystem processes (Fischer *et al.* 2010). Our study sites were located in three regions across Germany: The UNESCO Biosphere Reserve Schorfheide-Chorin (SCH) is located in the glacially formed lowlands in the state Mecklenburg-Vorpommern (3-140 m a.s.l.) in the North-East. The Hainich-Dün area (285-550 m a.s.l.), in the state Thuringia includes the UNESCO World Heritage Site National Park Hainich (HAI), one of the largest closed deciduous forest areas in Central Germany. The UNESCO Biosphere Reserve Swabian Alb (ALB) is located in the low mountain range in the state Baden-Württemberg (460-860 m a.sl) in the South-West. For more information of the project see (Fischer *et al.* 2010)

BeLongDead-Experiment

The BeLongDead-Experiment is a long-term experiment for the monitoring of deadwood decomposition and was established by the Biodiversity Exploratories project in 2009. In each study region three different forest management types with three replicates, 9 sites in ALB, HAI and SCH respectively, i.e. 27 sites in total, were chosen: (1) unmanaged European beech (*Fagus sylvatica*) dominated forest sites, which have been taken out of management 10 to 30 years ago, (2) managed age-class beech (*Fagus sylvatica*) forest sites, which are harvested at 80 – 120 year intervals, and (3) conifer plantations, including spruce (*Picea abies*) in HAI and ALB, and pine (*Pinus sylvestris*) in SCH.

On each 1 ha research plot three replicates (termed subplot hereafter) of freshly logged deadwood logs of 13 tree species (*Acer* sp.*, Betula pendula, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus* sp.*, Prunus avium, Pseudotsuga menziesii, Quercus* sp.*, Tilia* sp.) were placed in random order (Appendix III.A; FigA.1). Overall, 1,025 deadwood logs (342 logs in SCH and the ALB, 341 logs in HAI) of about 4 m length and 20 cm to 70 cm diameter were exposed. As one subplot is used as a control without experimental manipulations, we sampled two subplots with overall 688 logs. *Prunus* was missing on 12 out of 54 subplots and *Acer* was missing on 2 out of 54 subplots due to shortage in log availability.

For sampling of saproxylic beetles we used self-manufactured closed emergence eclectors, built up of a curved metal rail (width 32 cm) and a panel of black cotton on each side. The eclectors were screwed on the deadwood logs and sealed with polyurethane foam. On top of the eclectors a sampling jar with a transparent lid and two smaller ones at both ends of the metal rail were mounted, each filled with saturated NaCl-solution (Appendix III.A; Fig. A.1). Traps were emptied monthly from the beginning of April until the end of September in 2011. Sample material was stored in 70 % Ethanol. Beetles were sorted out in the lab and determined to species level by taxonomic specialists. We had to exclude all samples taken in August and September 2011 due to storm damage and severe loss of samples. Furthermore, we had to exclude all samples of the study plot 3 in the Swabian Alb due to storm damage. In the Swabian Alb three logs of *Pseudotsuga menziesii*, one log of *Carpinus betulus* and *Fagus sylvatica* were excluded because mice gnawed holes in the panels of the trap. For the same reason we had to exclude samples of one log of *F. sylvatica*, *Betula pendula* and *Picea abies* taken in Hainich-Dün.

Classification into guilds

Only saproxylic beetle species were selected for the analyses, non-saproxylic beetles, which made up 7% of the total amount of sampled beetles, were excluded. The classification of saproxylic beetles followed (Köhler 2000, supplemented by Schmidl and Bussler 2004). Furthermore, we classified sampled saproxylic beetles into different functional groups based on information about their nutritional ecology (Schmidl & Bussler 2004; Moeller 2009). The group of detritus consumers (saprophagous and necrophagous species) included only a few individuals and was therefore excluded from analyses. We distinguished between (1) primary consumers of woody material (“Xyl”), (2) consumers of fungi and mouldy material (“Myc”), and (3) predators (“Zoo”).

Statistics

All statistical analyses were performed using the software R 2.15.1 for statistical computing (R Core Team 2013).

We pooled sampled saproxylic beetle data of one log from the beginning of April 2011 until end of July 2011 in the analyses. According to Blüthgen *et al.* (2006) calculation of specialisation indices is critical for species representing just one individual in all samples. Therefore, we excluded overall 73 Singletons; 18 within the guild mycetophages, 22 within the guild xylophages and 33 within the guild predators. We considered the exposed deadwood logs of each study site as an independent network and pooled the data of the sampled saproxylic beetle species per plot for the calculation of quantitative network indices. For network analyses we choose network indices that are robust against variation in matrix size, shape, and sampling effort (Blüthgen *et al.* 2006; Dormann *et al.* 2009).

The network index H_2' is valuable to compare the degree of specialisation across different interaction webs. H_2' is the deviation of observed interactions from the expected interactions (Blüthgen *et al.* 2006). Complementary, the index d_i' measures the deviation of resource use from the expected distribution. Both indices range between 0 (perfect generalisation) and 1 (perfect specialisation). The range of the index network robustness is between 0 (fragile system) and 1 (stable system). Generality calculates the weighted mean effective number of saproxylic beetle species per tree species (Blüthgen *et al.* 2006; Dormann *et al.* 2009).

First, we calculated the network indices for the complete network per study site and in a second step we calculated all indices separately for networks of xylophages, mycetophages, and for predators per study site. To test whether network indices differed between the different guilds, we conducted mixed effect models with each network index as the response variable and guilds as predictor variables (levels “All”, “Xyl”, “Myc”, and “Zoo”), followed by a post-hoc Tukey test for multiple comparisons of means and the Benjamini & Hochberg (1995) adjustment method for p-values. To test whether forest type, study region, and a possible interaction of both parameters had a significant effect on network parameters within the different guilds, we calculated linear mixed effects models separately for xylophages, mycetophages, and predators with forest type, study region and their interaction as fixed effects and study site as random effect. Model simplifications were conducted via stepwise deletion of least significant terms, starting with the interaction term, according to Crawley (2007). To test whether host specificity of deadwood varied between tree species within the different guilds, we conducted linear effect models with the index d_i' as fixed effect and tree species identity as random effect separately for xylophages, mycetophages, and predators. The models were followed by a post-hoc Tukey test for multiple comparisons of means.

Results

Overall, we sampled 37,830 individuals of 323 saproxylic beetle species. Based on literature we assigned 37,776 individuals of 316 species as xylophages (7,570 individuals, 96 species), mycetophages (17,354 individuals, 84 species) or predators (12,852 individuals, 136 species).

Network structure

The mean overall specialisation (H_2') for interaction networks of saproxylic beetles was 0.54 ±0.21. In accordance with our expectations, network (H_2') and resource specialisation (d_i') were significantly higher for networks of xylophages compared to mycetophages and predators (Fig III.1a - b). Accordingly, network generality and robustness was significantly higher for predators and lowest for xylophages (Fig. III.1c - d). Many xylophages interact almost exclusively with few host tree species (Fig. III.2a), whereas a more generalistic behaviour towards the dead host trees is observed for mycetophages and predators (Fig. III.2b - c).

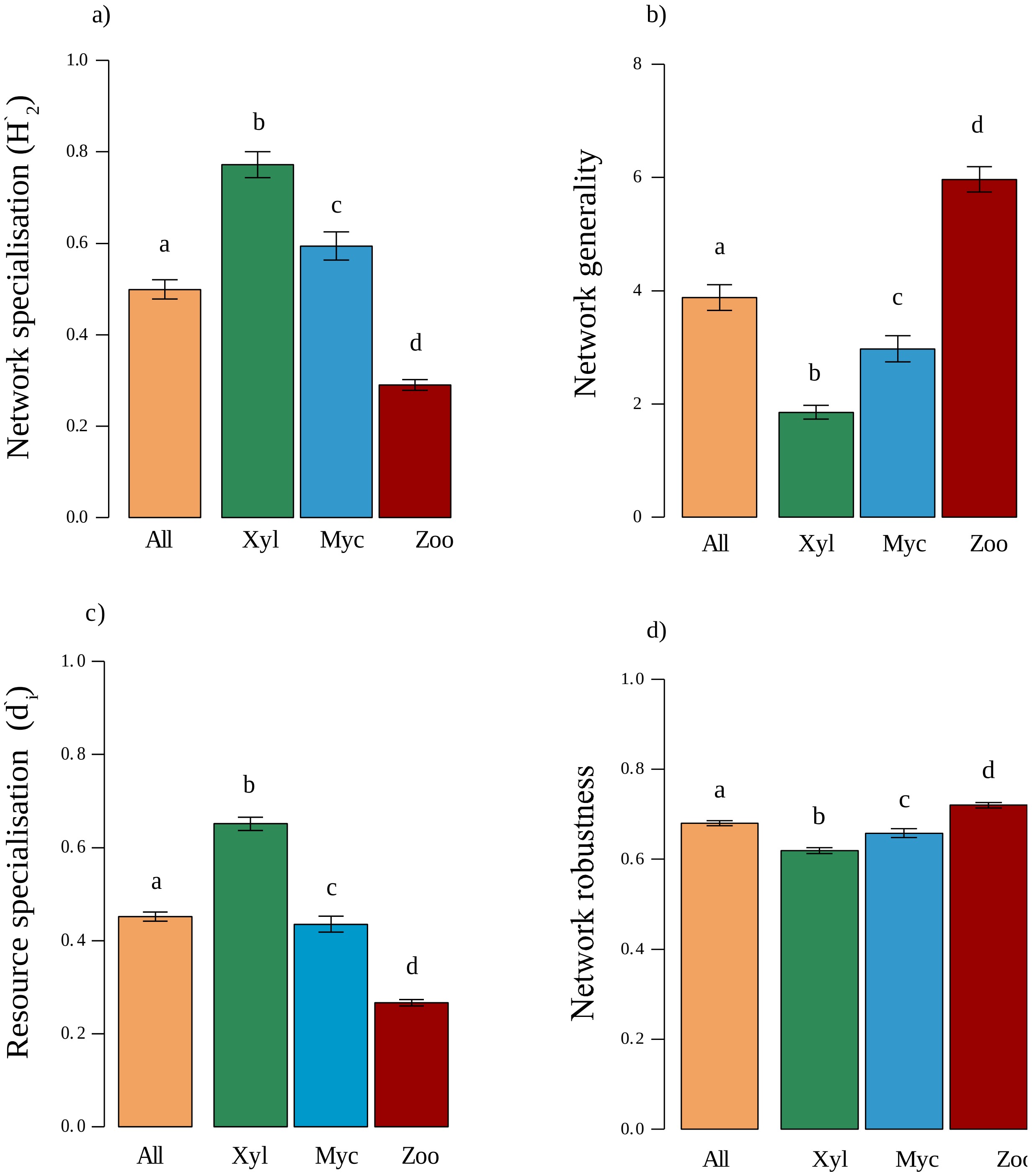


Fig. III.1: Weighted network indices for the different trophic guilds of saproxylic beetles (Xyl: xylophages; Myc: mycetophages; Zoo: predators). Different letters indicate significant differences.

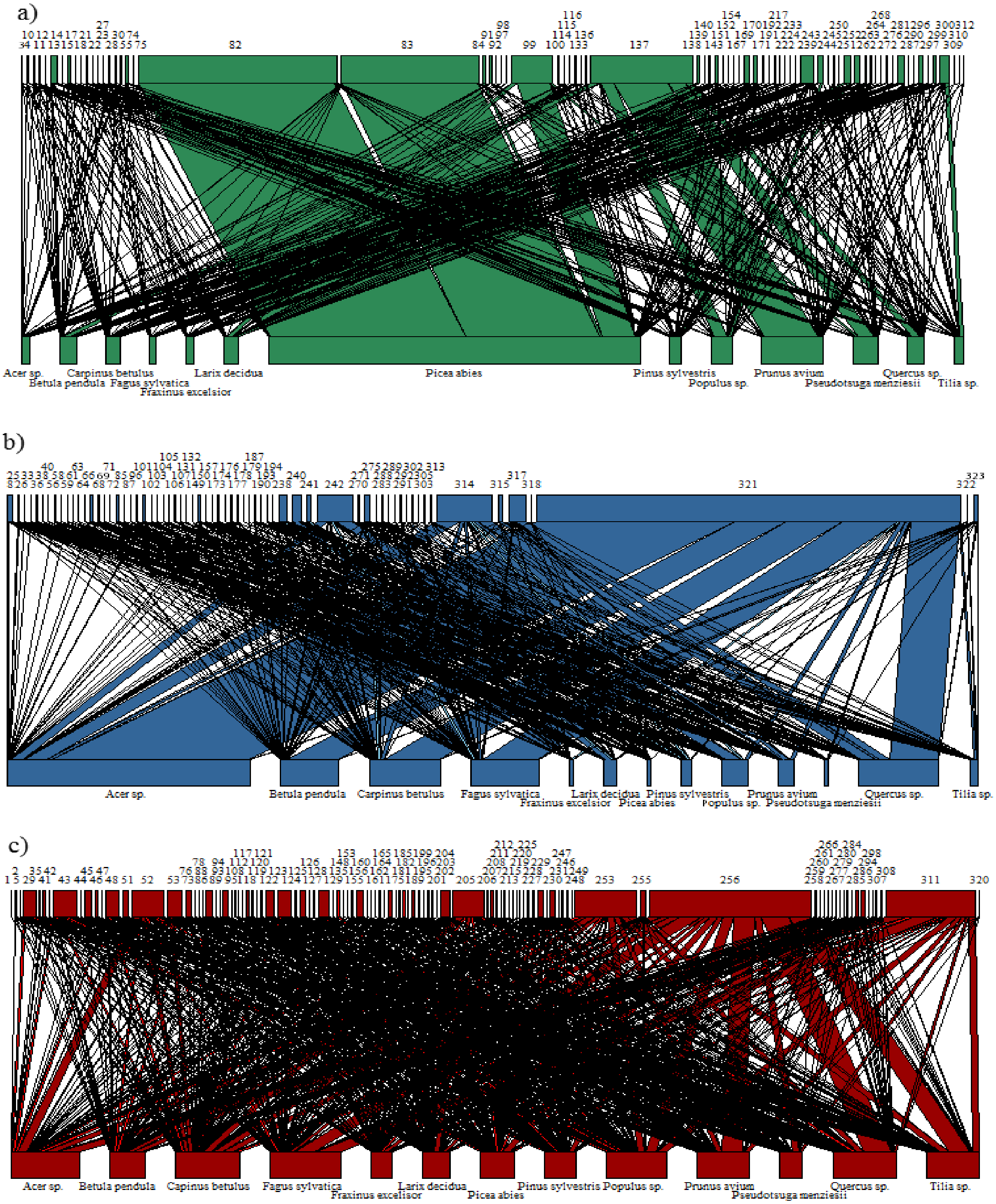


Fig. III.2: Species interaction networks for a) xylophages, b) mycetophages, and c) predators with deadwood of 13 tree species. Widths of links express interaction frequencies, bar sizes total interaction frequencies. Tree species are scaled in proportion to interactions with saproxylic beetles.

Forest type and study region had different effects on network indices within the different trophic guilds. Study region significantly affected network specialisation (H_2') within all trophic guilds and generality and resource specialisation (d_i') within xylophages and predators (Tab. III.1; and Appendix III.B; Fig. III.B.2). The interaction of forest type and study region was significant for network robustness of mycetophages (Tab. III.1). Additionally, forest type affected network robustness of xylophages and predators (Tab. III.1 and Appendix III.B; Fig.III.B.3).

Tab. III.1: Linear mixed effects models of network indices for saproxylic beetle networks of different trophic levels including all relevant covariates and interaction terms. Significant factors are in bold.

Indices		**NumDf**	**DenDF**	**F-value**	**p-value**
Network specialisation (H_2')	*Xylophages*				
	Region	2	23	10.34	**<.0001**
	Mycetophages				
	Region	2	23	5.95	**0.0083**
	Predators				
	Region	2	23	5.03	**0.0155**
Generality	*Xylophages*				
	Region	2	23	14.34	**<.0001**
	Mycetophages				
	Forest type	2	17	1.22	0.3203
	Region	2	17	0.22	0.8083
	Forest type : Region	4	17	1.34	0.2963
	Predators				
	Forest type	2	21	3.96	**0.0347**
	Region	2	21	6.92	**0.0049**

Tab. III.1 continued:

Indices		**NumDf**	**DenDF**	**F-value**	**p-value**
Resource specialisation (d'_i)	*Xylophages*				
	Forest type	2	17	0.10	0.9041
	Region	2	17	10.59	**0.0010**
	Forest type : Region	4	17	2.08	0.1283
	Mycetophages				
	Forest type	2	17	0.89	0.4290
	Region	2	17	2.15	0.1473
	Forest type : Region	4	17	1.66	0.2046
	Predators				
	Forest type	2	21	4.47	**0.0242**
	Region	2	21	6.30	**0.0072**
Network robustness	*Xylophages*				
	Forest type	2	23	4.95	**0.0163**
	Mycetophages				
	Forest type	2	17	9.66	**0.0016**
	Region	2	17	3.48	0.0541
	Forest type : Region	4	17	4.06	**0.0172**
	Predators				
	Forest type	2	21	5.03	**0.0165**
	Region	2	21	3.57	**0.0464**

Host specificity varied significantly between tree species within xylophages and mycetophages (Fig. III.3a-b). However, for the predator guild we found no significant difference in host specificity (Fig. III.3c). Logs of *P. abies* were significantly more host specific than logs of other tree species within the guild of xylophages. Additionally, host specificity of logs of *P. abies, L. decidua, Populus* sp., and *P. sylvestris* was significantly higher compared to other 9 tree species within mycetophages (Fig. III.3b). Resource specialisation was not correlated to the frequency of tree species occurrence ($p = 0.7834$; Appendix III.B; Fig.III.B.4).

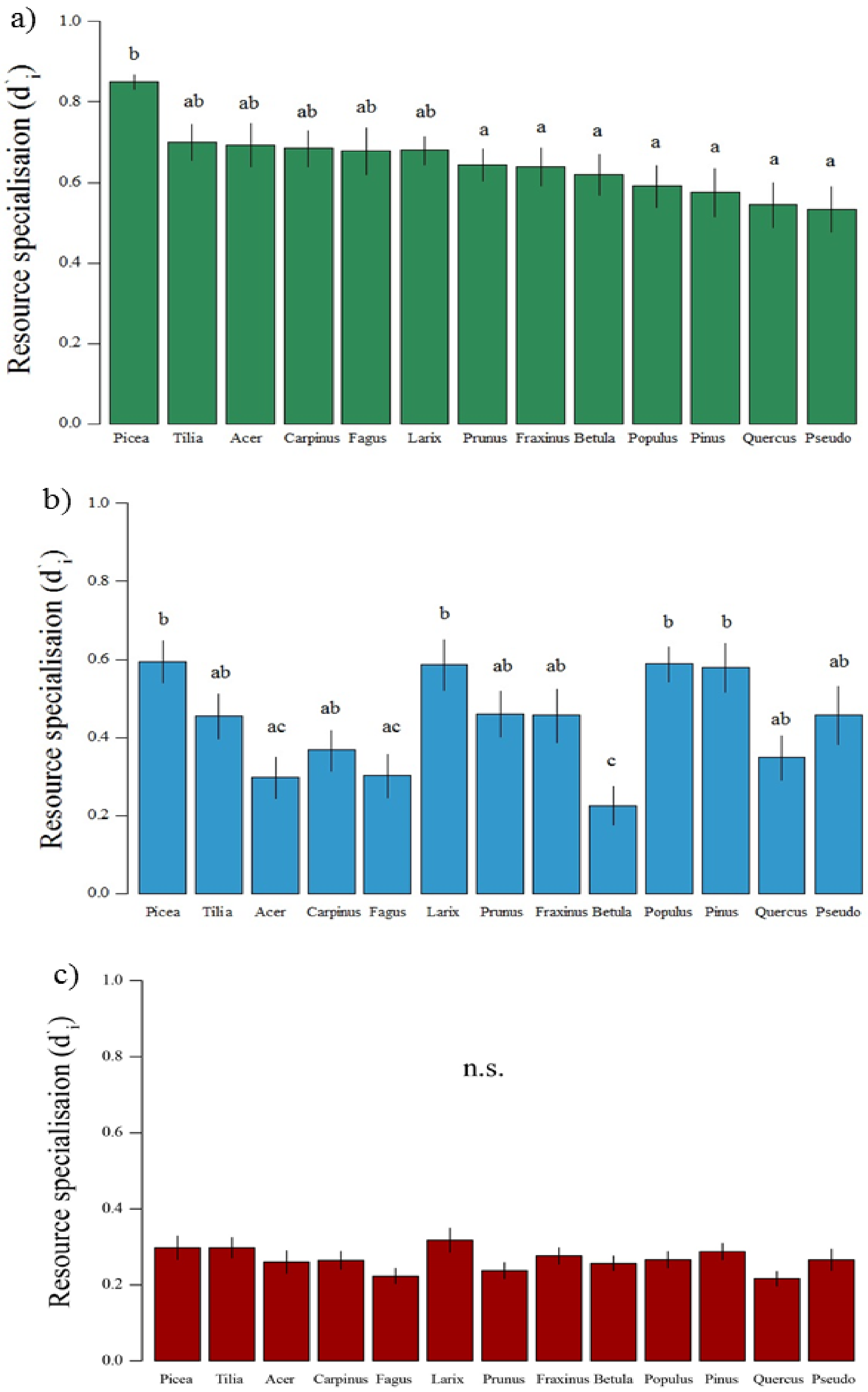


Fig. III.3: Differences in resource specialisation of saproxylic beetles between deadwood logs of 13 tree species for a) xylophages, b) mycetophages and c) predators.

Discussion

Our study analysed for the first time saproxylic beetle interaction networks with 13 dead host trees in temperate forest ecosystems. Overall, specialisation of saproxylic beetles was remarkably high and this result was consistent in three distinct regions. In particular, early successional wood-dependent beetle sub-guilds were more specialised than fungi-dependent and insect-dependent sub-guilds of higher trophic levels. Not intensive forest management but regional variation affected network specialisation.

In contrast to our expectations, mean specialisation value of 0.47 (SD = ± 0.13) of the trophic guild were generally high. Furthermore, compared to mutualistic interaction networks (values of 0.3 to 0.57 (Blüthgen *et al.* 2007; Boutin *et al.* 2010)), saproxylic beetle interaction networks were equally highly specialised. Specialists are often behaviourally, nutritionally and morphologically adapted to their hosts, which give them advantages for successful colonization, reproduction, and resource exploitation compared to generalists (Laverty & Plowright 1988). To prevent severe damage, plant defence comprises two major compounds; constitutive defence and induced defence. Long-living immobile chemicals supporting plant structure e.g. lignin or polyphenols, are part of the constitutive defence. Mobile chemicals (also termed volatile organic compounds), are introduced by the plant during herbivore attack (Coley *et al.* 1985). Contrary to the volatile organic compounds, which are depleted after few hours, immobile chemicals remain active after tree death. Due to the fact that these chemicals become poisonous via the absorbed dosage, adaptations for a higher tolerance or strategies to overcome the poisonous effects should give specialists vital advantages (Coley *et al.* 1985). Therefore, resource specialisation is probably more efficient than a more generalistic use of fresh wood resources (Montoya *et al.* 2006).

According to the resource-availability hypothesis of Coley et al. (1985) tree defence differs between fast and slow growing trees. Slow growing trees should invest more in the cost-intensive constitutive defence, whereas fast-growing trees should rely on induced herbivore defence via volatile organic compounds. Consistent with this assumption most interactions of xylophagous beetles were observed with deadwood of *Picea abies*, a valuable tree species for silviculture as it is fast growing and covers the largest area of living trees in German forests among studied tree species. Several studies reported a positive correlation between host specificity and plant frequency of occurrence (Chew & Courtney 1991; Brandle & Brandl

2001; Novotny & Basset 2005). Furthermore, to avoid the risk of going co-extinct, specialists should interact with a generalistic partner (Koh *et al.* 2004).

The plant-apparancy hypothesis of Levins and MacArthur (1969) proposes that high levels of defence are necessary in apparent plants to avoid suffering from herbivore damage and often only specialists are able to exploit these well-protected resources (Coley *et al.* 1985; Brandle & Brandl 2001). Accordingly, specialisation of the wood-dependent sub-networks of xylophages had significantly higher specialisation degrees than fungi-dependent and insect-dependent sub-networks. Secondary colonizers depend not solely on deadwood as resource, but also on the presence of prey of different taxa (Gibb *et al.* 2006b). Accordingly, the H_2`-value of the predator sub-guild was significantly lower than the other sub-guilds as the prey spectrum of the investigated saproxylic predators comprises not only beetles, but also springtails, dipteran larvae or mites.

In this study the relatively low specialisation values of predatory saproxylic beetles and colonizers of wood-decaying fungi might be influenced by the fact that we based our analyses of the interaction networks on tree species identity, which might not be the determining parameter for the specialisation degree of these guilds. Colonizers of wood-decaying fungi depend on their host fungal species, and the fungal community is in turn specialised on their host trees (Lonsdale *et al.* 2007).

Contrary to our expectations, we found no evidence that intensive forest management negatively affected network specialisation of the various sub-guilds. Regional differences were revealed to be important for the specialisation degree of saproxylic beetle species. Generally, lower specialisation and more generalistic species are expected in networks with many interactions due to many redundant species. This assumption may also explain the significantly lower specialisation value in Schorfheide-Chorin. A high specialisation degree is assumed to indicate interactions evolved between species over the long-term (Olesen & Jordano 2002; Guimarães *et al.* 2006). Furthermore, specialists tend to be more abundant in less disturbed habitats (Devictor *et al.* 2008). Evidence for both assumptions could be found in the Hainich-Dün region with the highest specialisation degree. Saproxylic beetle species might have found shelter in some refuges within the old-grown beech forest relicts (Fischer *et al.* 2010) and thereby were able to specialise on various host trees as the Hainich-Dün region comprises the largest connected semi-natural broadleaved forest in Germany with many rare tree species (Sobek *et al.* 2009). Furthermore, according to the resource-availability hypothesis local resource availability drives the extent of plant defence, so a more effective plant defence is expected in habitats with high resource availability (Coley *et al.* 1985). The three investigated regions differ in their soil types. Schorfheide-Chorin is geologically dominated by glacial till; its soils have a texture from sandy loam to pure sand, which explains the high frequency of pine forests in the region (Fischer *et al.* 2010). In contrast, loess is the most frequent substrate with loamy or clayey texture in the Hainich-Dün region and its soils are very fertile. The soils in the Swabian Alb are rich in clay as they developed on Jurassic shell limestone and are often used as sheep pastures as they do not support intensified land types (Fischer *et al.* 2010). Due to the fact that the soils in the Hainich-Dün region support good resource availability, tree species should be able to invest more in cost-intensive and long-living chemical defence such as lignin. As mentioned above, specialists are most suitable to overcome chemical barriers of the woody material.

We conclude that saproxylic beetle species of different sub-guilds are more threatened by species loss than previously assumed due to the overall high degree of specialisation. As several studies have shown, protecting interaction networks within ecosystems are a valuable method to conserve the participating species and thereby ecosystem function (Devoto *et al.* 2012). Due to the fact that specialisation degree of saproxylic organisms depends on tree species, high deadwood diversity in all its forms is necessary to cover all required habitats.

Appendix III.A

Table III.A1: Number of deadwood logs and number and abundance of saproxylic beetle species, saproxylic in the study regions, the different forest types, and tree species without the excluded samples due to trap damage.

		Number of experimental logs	**Species Number/ abundance of saproxylic beetles**
Region	Swabian Alb	199	107 / 9,821
	Hainich-Dün	222	143 / 15,614
	Schorfheide-Chorin	230	264 / 12,395
Forest type	Beech age class forest	227	208 / 13,318
	Unmanaged forest	172	183 / 6,755
	Conifer age class forest	252	257 / 17,757
Tree species	*Acer* sp.	50	127 / 8,491
	Betula pendula	51	135 / 2,644
	Fagus sylvatica	50	133 / 3,519
	Pseudotsuga menziesii	47	105 / 905
	Quercus sp.	52	136 / 3,893
	Fraxinus excelsior	51	113 / 675
	Picea abies	51	155 / 5,622
	Carpinus betulus	51	155 / 3,616
	Prunus avium	41	122 / 2,356
	Pinus sylvestris	52	131 / 1,135
	Larix decidua	52	127 / 1,154
	Tilia sp.	51	136 / 1,518
	Populus sp.	52	119 / 2,302

Table III.A2: List of saproxylic beetle species and reference numbers of the interaction networks.

Saproxylic beetle species	Number	Saproxylic beetle species	Number
Abraeus granulum	1	*Cis hispidus*	59
Abraeus perpusillus	2	*Cis micans*	61
Acalles camelus	3	*Cis punctulatus*	63
Acalles hypocrita	4	*Cis rugulosus*	64
Acritus minutus	5	*Corticaria abietorum*	66
Agathidium nigripenne	8	*Corticaria linearis*	68
Ampedus balteatus	10	*Coricaria longicollis*	69
Ampedus cinnabarinus	11	*Corticarina lambiana*	71
Ampedus elongatulus	12	*Corticarina obfuscata*	72
Ampedus pomorum	13	*Corticeus unicolor*	73
Ampedus rufipennis	14	*Corymbia rubra*	74
Ampedus sanguineus	15	*Corymbia scutellata*	75
Anaspis flava	17	*Coryphium angusticolle*	76
Anaspis frontalis	18	*Cryptolestes duplicatus*	77
Anaspis ruficollis	21	*Crypturgus cinereus*	82
Anaspis rufilabris	22	*Crypturgus hispidulus*	83
Anaspis thoracica	23	*Crypturgus pusillus*	84
Anisotoma humeralis	25	*Cychramus variegatus*	85
Anisotoma orbicularis	26	*Cyphea curtula*	86
Anobium costatum	27	*Dacne bipustulata*	87
Anobium pertinax	28	*Dadobia immersa*	88
Anomognathus cuspidatus	29	*Dasytes aeratus*	89
Anthribus albinus	30	*Denticollis linearis*	91
Arpidiphorus orbiculatus	33	*Denticollis rubens*	92
Atheta picipes	35	*Dexiogya corticina*	93
Atomaria bella	36	*Dinaraea aequata*	94
Atomaria procerula	38	*Dinaraea linearis*	95
Atomaria umbrina	40	*Diplocoelus fagi*	96

Atrecus affinis	41	*Dissoleucas niveirostris*	97
Batrisodes venustus	42	*Dorcus parallelipipedus*	98
Bibloporus bicolor	43	*Dryocoetes autographus*	99
Bibloporus mayeti	44	*Dryocoetes villosus*	100
Bibloporus minutus	45	*Endomychus coccineus*	101
Bitoma crenata	46	*Enicmus atriceps*	102
Bolitochara lucida	47	*Enicmus brevicornis*	103
Bolitochara obliqua	48	*Enicmus fungicola*	104
Cerylon fagi	51	*Enicmus planipennis*	105
Cerylon ferrugineum	52	*Enicmus testaceus*	106
Cerylon histeroides	53	*Ennearthron cornutum*	107
Choragus sheppardi	55	*Epuraea limbata*	108
Cis boleti	56	*Epuraea pygmaea*	112
Cis glabratus	58	*Ernobius mollis*	114
Ernobius nigrinus	115	*Micridium halidaii*	174
Ernoporicus fagi	116	*Microscydmus minimus*	175
Euplectus brunneus	117	*Mycetina cruciata*	176
Euplectus decipiens	118	*Mycetophagus atomarius*	177
Euplectus fauveli	119	*Mycetophagus fulvicollis*	178
Euplectus infirmus	120	*Mycetophagus quadripustulatus*	179
Euplectus karsteni	121	*Nemosoma elongatum*	181
Euplectus kirbyi	122	*Neuraphes carinatus*	182
Euplectus nanus	123	*Nudobius lentus*	185
Euplectus piceus	124	*Octotemnus glabriculus*	187
Euplectus punctatus	125	*Opilo mollis*	189
Euplectus tholini	126	*Orchesia micans*	190
Euryusa castanoptera	127	*Orchesia minor*	191
Gabrius splendidulus	128	*Orchesia undulata*	192
Glischrochilus quadripunctatus	129	*Orthocis alni*	193
Gyrophaena boleti	131	*Orthocis festivus*	194

Gyrophaena minima	132
Hedobia imperialis	133
Homalota plana	135
Hylastes attenuatus	136
Hylecoetus dermestoides	137
Hylesinus crenatus	138
Hylis cariniceps	139
Hylis foveicollis	140
Hylurgops palliatus	143
Laemophloeus monilis	148
Latridius consimilis	149
Latridius hirtus	150
Leiopus nebulosus	151
Leperisinus fraxini	152
Leptoplectus spinolae	153
Leptura quadrifasciata	154
Leptusa fumida	155
Leptusa pulchella	156
Litargus connexus	157
Malthinus punctatus	160
Malthodes crassicornis	161
Malthodes guttifer	162
Malthodes pumilus	164
Malthodes spathifer	165
Melandrya barbata	167
Melanotus castanipes	169
Melanotus rufipes	170
Melasis buprestoides	171
Micrambe abietis	173
Ptinella aptera	240
Ptinella limbata	241
Orthoperus atomus	195
Orthoperus mundus	196
Oxypoda recondita	199
Paromalus flavicornis	201
Paromalus parallelepipedus	202
Pediacus depressus	203
Phloeocharis subtilissima	204
Phloeonomus punctipennis	205
Phloeonomus pusillus	206
Phloeopora corticalis	207
Phloeopora testacea	208
Phyllodrepa ioptera	211
Phyllodrepa linearis	212
Phyllodrepa nigra	213
Pityophagus ferrugineus	215
Pityophthorus pityographus	217
Placonotus testaceus	219
Placusa atrata	220
Platycerus caraboides	222
Platyrhinus resinosus	224
Platysoma compressum	225
Plectophloeus fischeri	227
Plectophloeus nitidus	228
Plectophloeus nubigena	229
Plegaderus caesus	230
Plegaderus dissectus	231
Pogonocherus fasciculatus	233
Pteryx suturalis	238
Ptilinus pectinicornis	239
Sulcacis affinis	291
Tachyta nana	294

Ptinella tenella	242
Pyrochroa coccinea	243
Pyrrhidium sanguineum	244
Pytho depressus	245
Quedius maurus	246
Quedius scitus	247
Quedius xanthopus	248
Rabocerus foveolatus	249
Rhagium bifasciatum	250
Rhagium inquisitor	251
Rhagium mordax	252
Rhizophagus bipustulatus	253
Rhizophagus depressus	255
Rhizophagus dispar	256
Rhizophagus nitidulus	258
Rhizophagus parvulus	259
Rhizophagus perforatus	260
Rhizophagus picipes	261
Rhyncolus ater	262
Rhyncolus elongatus	263
Rhyncolus sculpturatus	264
Salpingus planirostris	266
Salpingus ruficollis	267
Saperda scalaris	268
Scaphidium quadrimaculatum	270
Scaphisoma agaricinum	271
Schizotus pectinicornis	272
Sepedophilus testaceus	275
Serropalpus barbatus	276
Siagonium quadricorne	277
Taphrorychus bicolor	296
Silvanus unidentatus	280
Sinodendron cylindricum	281
Sphindus dubius	283
Stenagostus rhombeus	284
Stenichnus bicolor	285
Stenichnus godarti	286
Stenostola dubia	287
Stephostethus alternans	288
Stephostethus rugicollis	289
Stereocorynes truncorum	290
Sulcacis fronticornis	292
Thanasimus formicarius	297
Tillus elongatus	298
Tomoxia bucephala	299
Trachodes hispidus	300
Triphyllus bicolor	302
Triplax aenea	303
Tritoma bipustulata	305
Tyrus mucronatus	307
Uleiota planata	308
Uloma culinaris	309
Variimorda fasciata	310
Vincenzellus ruficollis	311
Xestobium plumbeum	312
Xyleborus dispar	313
Xyleborus germanus	314
Xyleborus monographus	315
Xyleborus saxeseni	317
Xylita laevigata	318

Silvanus bidentatus	279
Xyloterus domesticus	321
Xyloterus lineatus	322
Xyloterus signatus	323
Xylostiba monilicornis	320

Appendix III.B

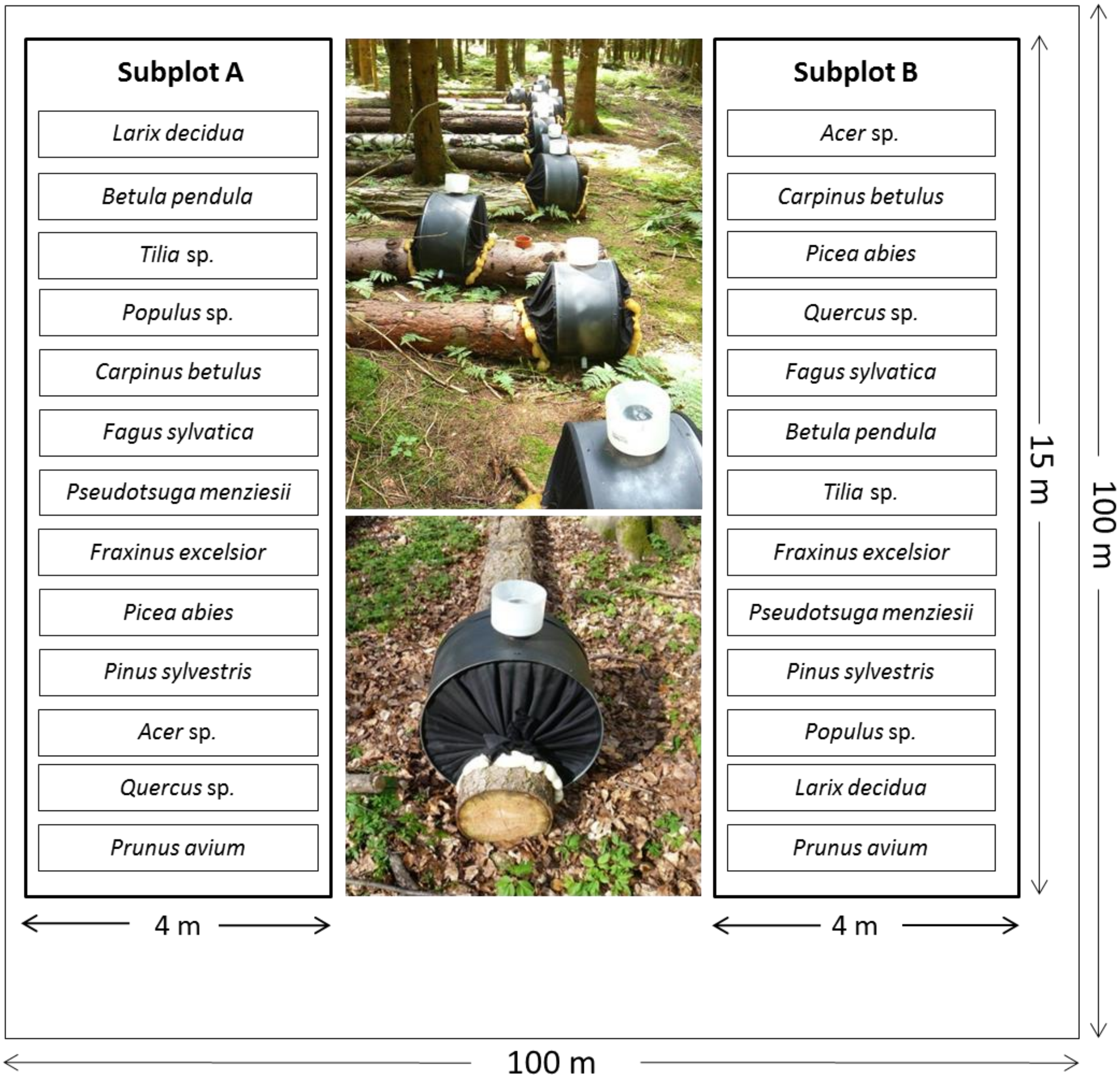


Fig. III.B1: General plot design with experimental subplots.

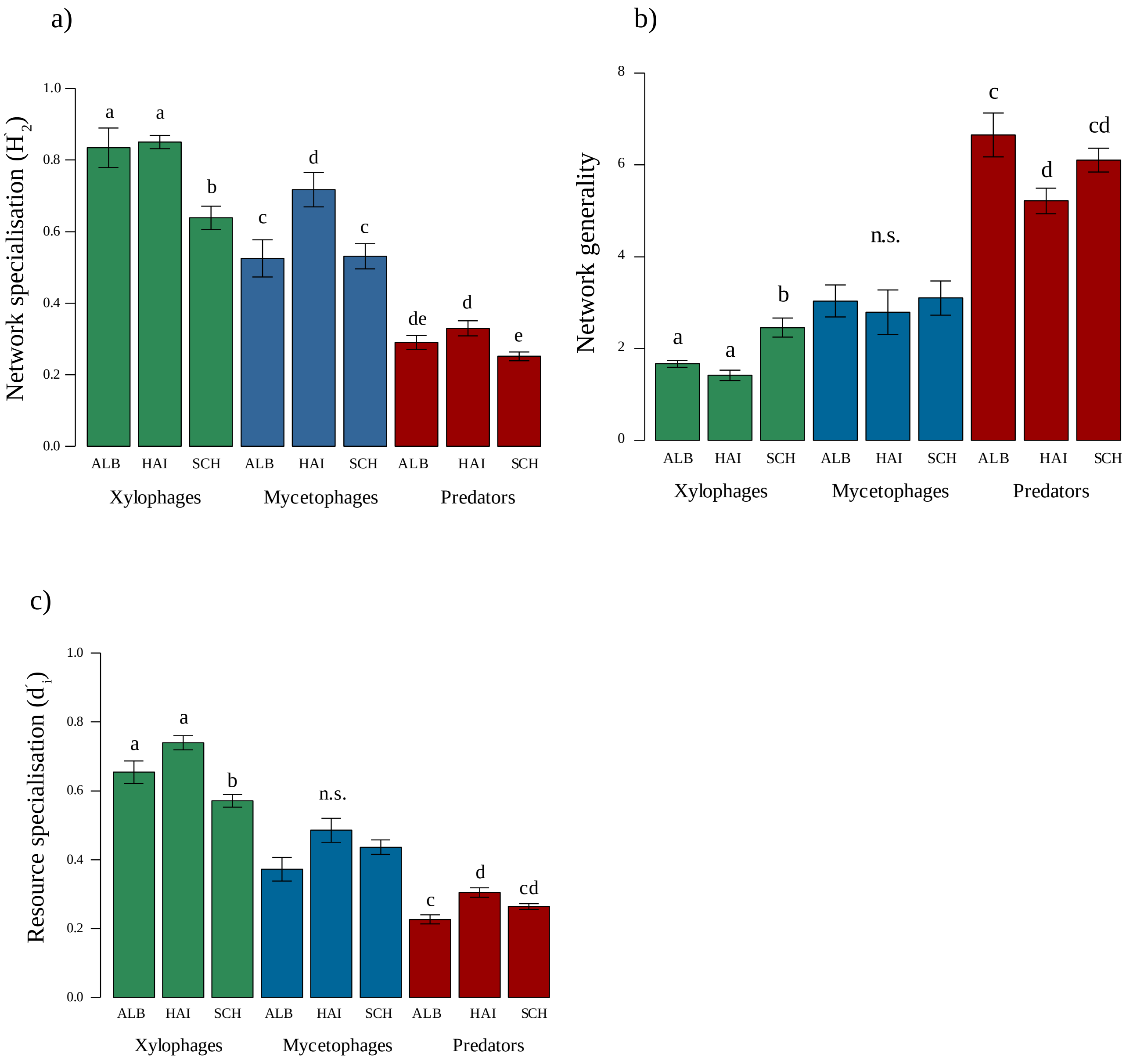


Fig. III.B2: Comparison of a) network specialisation, b) generality and c) resource specialisation between the three regions for the different trophic levels of saproxylic beetles (ALB: Swabian Alb, HAI: Hainich-Dün, SCH: Schorfheide-Chorin). Mean values per region, error bars show S.E., different characters indicate significant differences.

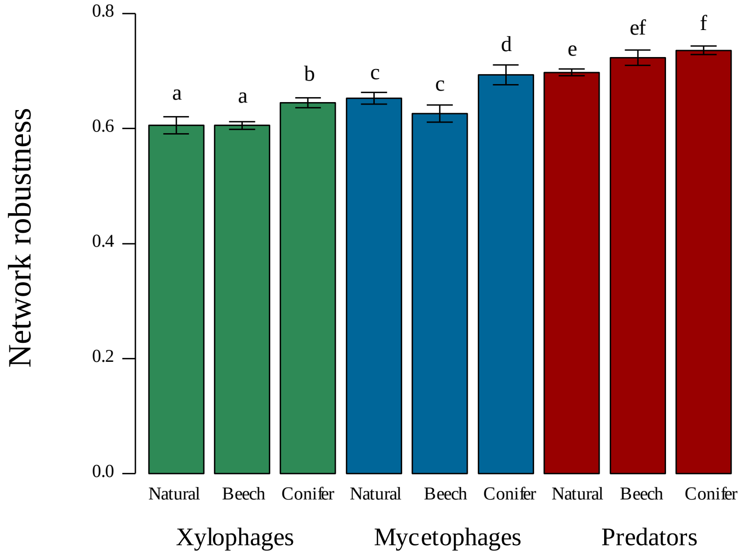


Fig. III.B.3: Comparison of network robustness between the three forest types for the different trophic levels of saproxylic beetles (Natural: unmanaged beech forests, Beech: beech age class forests, Conifer: Conifer age class forests). Mean values per forest type, error bars show S.E., different characters indicate significant differences.

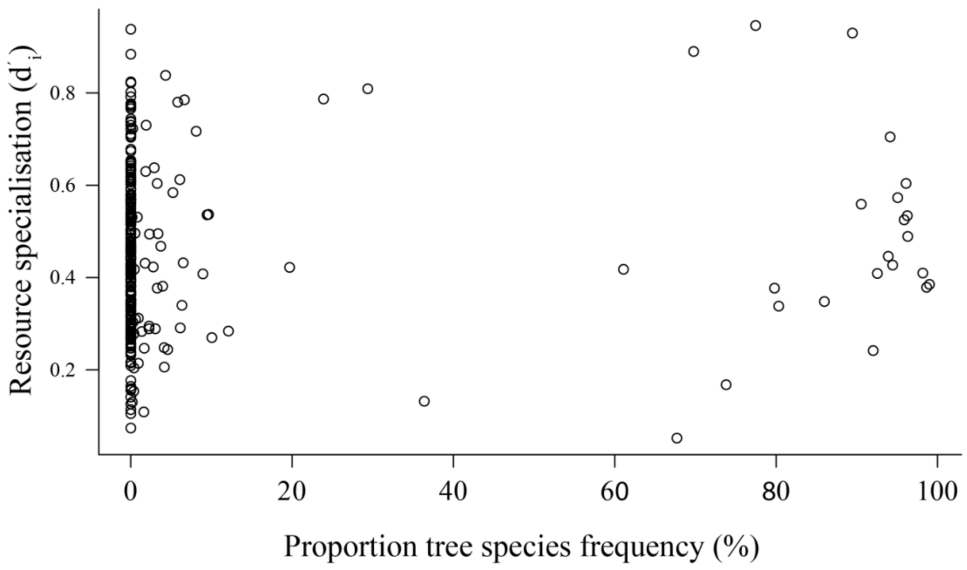


Figure III.B.4: Correlation of frequency of tree species occurrence per study plot and resource specialisation (d'_i).

CHAPTER IV: LOCAL STAND FACTORS, LANDSCAPE COMPOSITION AND GEOGRAPHICAL CONDITIONS AFFECT DIVERSITY OF SAPROXYLIC BEETLE GUILDS

Abstract

Intensified management substantially altered structure and composition of European forest landscapes, resulting in an increased number of endangered beetle species inhabiting deadwood. Though the importance of deadwood characteristics on species richness of saproxylic beetles has been investigated, the effects of environmental factors at larger spatial scales were rarely addressed. Therefore, we investigated the relationship of 14 environmental factors on diversity of early, intermediate and late successional saproxylic beetles at three spatial scales: local stand factors at a 0.1 km radius, landscape composition at a 2 km radius, and abiotic conditions in 400 km to 700 km distance. We exposed 688 deadwood logs of 13 tree species at 27 forest sites in three distinct regions and sampled hatching saproxylic beetle species via closed emergence traps. On local and landscape scale parameters indicating fragmentation negatively affected saproxylic species richness within each investigated guild. However, species richness of intermediate and advanced successional decay stages decreased with locally increasing deadwood amount and increasing area of arable land in the surrounding landscape of the study site. Across all guilds, saproxylic species richness increased along warmer climatic conditions, but decreased with increasing humidity. We conclude that guild-specific requirements of saproxylic beetle species on larger spatial scales should be integrated in the development of conservation orientated sustainable forest management practices.

Keywords

species richness; stand structure; landscape composition; deadwood; fragmentation; forest ecology

Introduction

In Europe, 80 % of the around 420 million hectares of European land (EU 27) are dedicated to agricultural production (43 %) and forestry (40 %) (European Environment Agency 2007). Thus, pristine habitats are very rare, for instance, less than 1% of European forests are classified as primeval (Paillet *et al.* 2010). Cultivation and management are often accompanied by profound consequences for the diversity of many taxa and related ecosystem services (Montoya *et al.* 2006; Worm *et al.* 2006; Phalan *et al.* 2011).

Forests provide many essential ecosystem services, e.g. air purification, carbon storage, preservation of freshwater resources, mitigation of soil erosion, and production of wood (Foley *et al.* 2005; Kremen 2005). However, the key process for the maintenance of nutrient cycling and the long-term fertility of forest soil, thereby sustaining forest ecosystem functions, is the decomposition of deadwood material (Ulyshen 2013). Nearly 25% of forest biota participates in the decomposition process (Jonsson *et al.* 2005). Saproxylic beetles play key role in deadwood decomposition. They serve as main vectors for fungal spores, and enhance habitat conditions for fungal growth due to their tunnelling and gnawing activities (Speight 1989).

However, intensification of silviculture has caused a notable decline within the saproxylic beetle community with 14% of all European saproxylic beetle species being listed on the European Red List in 2010 (Nieto & Alexander 2010). Reduced local deadwood amount is considered a main reason as managed temperate forests provide only 2-15 m^3/hectare compared to 60-90 m^3/hectare in pristine forests of Eastern Europe (Siitonen 2001; Merganičová *et al.* 2012). Moreover, silvicultural management prevent the development of advanced decayed deadwood habitats as mature trees are felled and logging residues only of small diameter are left on the forest sites (Gibb *et al.* 2005). Thus, many studies concerning conservation strategies for saproxylic biodiversity investigated the effects of local stand factors e.g. deadwood quantity and deadwood quality in terms of diameter, decay stage and/or vertical and horizontal distribution (Jonsell & Weslien 2003; Jonsell *et al.* 2007; Djupström *et al.* 2008; Brin *et al.* 2010).

Saproxylic beetles can be subdivided in groups of functionally similar species (guilds) colonizing either early, intermediate or advanced decayed deadwood, thereby mirroring a successional gradient in substrate preference (Moran & Southwood 1982). Due to different habitat requirements, it is likely that environmental parameters affect saproxylic guilds differently (Lassau *et al.* 2005; Johansson *et al.* 2007a; Woodcock *et al.* 2009).

However, in contrast to agricultural landscapes (Blitzer *et al.* 2012) effects of forest landscape composition and regional varying abiotic conditions on saproxylic beetle diversity of different guilds remained largely untested (Gibb *et al.* 2006a; Franc *et al.* 2007). Therefore, we analysed in this large-scale study the effects of environmental factors at three different spatial scales on saproxylic beetle diversity. More specifically, we used data of saproxylic beetle species colonizing 688 experimentally exposed deadwood logs in a total of 27 forest sites. We predict that (1) local stand factors and (2) increasing amounts of non-forest area on landscape scale affect saproxylic beetles of intermediate and late decay stages stronger than early successional stages. Furthermore, (3) species richness of saproxylic beetle guilds increases in warmer climatic conditions, as being ectotherms their physical activities depend on the ambient temperature.

Material and methods

Biodiversity Exploratories

Our study was conducted in the framework of the Biodiversity Exploratories (www.biodiversity-exploratories.de), comprising three study regions: (1) The glacially formed UNESCO Biosphere Reserve Schorfheide-Chorin (SCH) located in the lowlands (3-140 m a.s.l.) in the North-East (longitudes 14.1° E to 13.4° W, latitudes 53.2° N to 52.8° S); (2) the Hainich-Dün area (285-550 m a.s.l.) including the UNESCO World Heritage Site National Park Hainich (HAI) in the hilly lands of Central Germany (285-550 m a.s.l.; longitudes 10.8° E to 10.2° W, latitudes 53.4° N to 50.9° S); (3) the UNESCO Biosphere Reserve Swabian Alb (ALB) located in the low mountain range (460-860 m a.sl) in the South-West (longitudes 6.6° E to 9.2° W, latitudes 48.5° N to 48.3° S) of Germany. The most frequent tree species on the study sites was European beech (*Fagus sylvatica*), followed by spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Pine forests occurred only in Schorfheide-Chorin, whereas spruce forests were restricted to Hainich-Dün and the Swabian Alb (Fischer *et al.* 2010). In 2012 a forest inventory of each study site, based on five circular sampling subplots (r= 12,62 m) was conducted and the tree composition recorded (Schall & Ammer 2013).

BeLongDead-Experiment

Our analyses were based on the data collected by the "BeLongDead"-project, a long-term experiment to monitor deadwood decomposition. In each study region nine 1 ha study sites were chosen, resulting in a total of 27 sites. In 2009 freshly logged (winter 2008/2009) deadwood logs of 13 different tree species (*Acer* sp., *Betula pendula, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus* sp., *Prunus avium, Pseudotsuga menziesii, Quercus* sp., *Tilia* sp.) were placed in random order on two subplots per study sites (Appendix IV.B; Fig. IV.B.1). Due to a shortage of *P. avium* overall 12 logs were missing*:* five in ALB, three in HAI and four in SCH. For the same reason two logs of *Acer* were missing in HAI. To minimize possible effects due to variation of origin, all logs (length of 4 m and diameter between 20 cm to 70 cm) were cut in the state of Thuringia and transported to all study plots.

Sampling design

For sampling of saproxylic beetles we used closed emergence eclectors built up of a curved metal rail (width 32 cm) with panels of black cotton on each side to allow some air circulation beneath the trap (Supplementary material, Appendix IV.B; Fig. B1). Compared to flight interception traps and trunk-window traps, eclectors are very selective and capture only species emerging from the deadwood substrate (Jonsson *et al.* 2005). Furthermore, eclectors are a non-invasive method, contrasting to woody debris dissection, and the deadwood has not to be removed from forest sites as it is necessary for ex situ rearing (Alinvi *et al.* 2006). In spring 2011, the eclectors were screwed on each exposed dead (N=688) wood log and sealed with polyurethane foam. At this time, all deadwood logs were in decay class II (bark and texture intact, original colour of wood) after classification of Bobiec et al. (2005). A sampling jar with a transparent lid filled with saturated NaCl-solution was mounted on top of the trap for the catching of light-attracted species. Additionally, two smaller sampling jars were placed on each end of the metal rail for the catching of bark crawling species. Traps were emptied monthly from the beginning of April until end of September 2011. Due to storm we lost many samples in August and September 2011. As the number of saproxylic beetle individuals caught in August (N=1,354) and September (N=508) made up only 5% of the total amount, we decided to exclude all samples taken in August and September. Furthermore, we had to exclude all samples of study plot 03 in the Swabian Alb due to storm damage in May 2011. For analyses, we pooled all samples from the beginning of April until end of July 2011 of the closed emergence traps for each study site**.** Sample material was stored in 70 % Ethanol. Beetles were sorted out in the lab and determined to species level by taxonomic specialists. We excluded non-saproxylic beetles from all statistical analyses, which made up 7% of all specimens**.** The classification in saproxylic beetles and non-saproxylic beetle species followed Köhler (2000) supplemented by Schmidl and Bussler (2004). The sampled saproxylic beetle species were then classified according to their calculated niche position (Gossner *et al.* 2013). We distinguished between beetle species inhabiting deadwood substrate of early (“Early”), intermediate (“Intermediate”), and advanced (“Advanced”) decay stages (Appendix IV.A; Tab. IV.A2).

Environmental variables

In total 16 parameters at three different spatial scales (6 parameters on local and landscape scale, and 4 parameters on regional scale) were chosen to evaluate their effects on diversity of three saproxylic beetle habitat guilds (Tab. IV.1).

Local stand factors

In 2007 and 2008 an inventory of the vegetation was carried out in an area of 20 m × 20 m on each study site. All vascular plants were identified and the percentage cover per species for tree layer (>10 m) was estimated (Boch *et al.* 2013). The variables “Tree cover”, “Proportion conifers”, and “Plant diversity” are based on this inventory. The parameters “DBH”, “Stand density”, and “Tree diversity” are based on a forest inventory in 2008 and 2009 on each study site within an area of 500 m^2 (Fischer *et al.* 2010; Hessenmöller *et al.* 2011; Schall & Ammer 2013). The variable „Deadwood amount“ is based on an additional deadwood inventory with a stratified sampling design and recording of all large standing and downed deadwood (>25 cm diameter) and estimating small downed deadwood (>7 and <25 cm) on each study site was conducted in in spring and summer 2012 (Kahl & Bauhus 2014).

Tab. IV.1: Investigated environmental variables of the different spatial scales.

Variable	Explanation
Local stand factors	
Deadwood amount	Deadwood amount per site (m^3/ha)
DBH	Mean diameter at breast height of all standing trees on the study site (1 ha) with diameter > 7cm
Plant diversity	Shannon index of all plants (herbs, shrubs and trees) recorded on each study site (1 ha)
Proportion conifers	Proportion of living conifer trees on each study site (1 ha)
Tree cover	Cover (%) of the tree layer for trees with height> 10m
Tree diversity	Shannon index of tree species recorded on each study site (1ha)
Landscape Scale	
Area arable land	Area (m^2) used for production of crops, vegetables, fruits, flowers and bare ground within 2 km radius of the study sites
Area forest	Area (m^2) that contains all forests, groups of trees, and single trees and shrubs within 2 km radius of the study sites
Area grassland	Area (m^2) contains all pastures, meadows, and heathlands within 2 km radius of the study sites
Area nature reserve	All nature protection area (m^2) within 2 km radius of the study sites
Area urban land	Area (m^2) that contains all sealed surface (villages, towns etc.) within 2 km radius of the study sites
Area wetlands	Area (m^2) that contains all-season wet ground, seasonal wet ground (marsh, bog etc.) and linear water wider than 12 m within 2 km radius of the study sites
Edge density	Sum of all edge lengths (m) of arable, urban, forest area, wetland, grassland, and nature reserve area within 2 km radius of the study sites
Regional Scale	
Altitude	Altitude (above sea level) of each study site
Humidity	Mean air moisture (%), measured weekly at 2 m above ground
Temperature (200)	Mean temperature (°C), measured weekly at 2 m above ground

Landscape composition

Landscape features were analysed via ArcGis (ArcMap 9.3) based on digital landscape maps (DLM). We choose a buffer with 2 km radius with the centre of the study site as centre of the buffer. For analysis we distinguished between the habitats arable land, grassland, forests, urban area, nature reserves and wetlands (Tab. IV.1). Additionally, we calculated the sum of the length of each habitat border within a 2 km radius around the centre of the study sites as a measure for the degree of fragmentation (Tab. IV.1).

Geographic conditions

The altitude of each study plot was calculated with coordinates of the plot on www.mapcoordinates.net. In all study plots monitoring units were set up 2 m above ground to measure climatic conditions. Air moisture and air temperature was measured hourly via data loggers (Fischer *et al.* 2010). The data were pooled and the mean value was calculated.

Statistics

All statistical analyses were performed with the software R (R version 3.0.2; R Core Team, 2013). To check for spatial autocorrelation for close-by study plots a mantel test with 999 permutations was performed (package vegan; (Oksanen 2009). Spatial distance (degree of latitude and longitude) of each plot was correlated to the saproxylic beetle community dissimilarity matrix (Bray-Curtis dissimilarity) per study plot by using the Bray-Curtis dissimilarity and the Euclidean distance for the spatial variability.

We calculated the variance inflation factor (VIF) to reveal possible collinearity among the environmental parameters on the local, landscape and regional scale, respectively (Dormann *et al.* 2013). The threshold for non-collinearity is a VIF-value less than 3. At local scale, the calculated variance inflation factor (VIF) of the parameters “Proportion understory” and “Stand density” were 9.7 and 5.1, respectively. “Proportion understory” was correlated to “Plant diversity”, and “Stand density” to “Tree cover”. Therefore, both variables were excluded from further analyses. As the calculated VIF-value of “Area grassland” was 4.7, this variable was excluded from further analysis. At regional scale, “Altitude” was highly correlated to “Temperature” and “Humidity” (VIF-Value = 73.1), and excluded from further analyses (Appendix IV.A; Tab. IV.A1).

We analysed effects of environmental variables on saproxylic beetle species richness of the different guilds by conducting linear mixed effects models (package nlme, Pinheiro et al., 2013). For each saproxylic beetle guild linear effects models were separately calculated for each spatial scale with the respective environmental variables as fixed factors and study site as random factor. Model simplifications were conducted via stepwise deletion of least significant terms, according to Crawley (2007). Multiple regression was conducted to check for differences of the environmental variables between the study regions, followed by post-hoc Tukey test for multiple comparisons of means (package multcomp; Hothorn et al., 2008) (Appendix IV.B; Fig. IV.B2). When environmental parameters differed significantly between the study regions, the respective interaction term was included in the models.

Results

Overall, we caught 37,830 saproxylic beetles representing 323 species and 54 families on deadwood logs (N=651) of 13 tree species. The highest abundance of saproxylic beetles was sampled in Hainich-Dün (N= 15,614), whereas most species were found in Schorfheide-Chorin (N= 264) (Appendix IV.A; Tab. IV.A2). 272 species (36,823 individuals) could be classified as either early successional, intermediate, or advanced successional beetles (Supplementary material Appendix IV.A, Tab IV.A3). In each guild species richness was significantly highest in Schorfheide-Chorin. Between Hainich-Dün and the Swabian Alb no significant difference was found (Fig. IV.1; Appendix IV.A; Tab. A2).

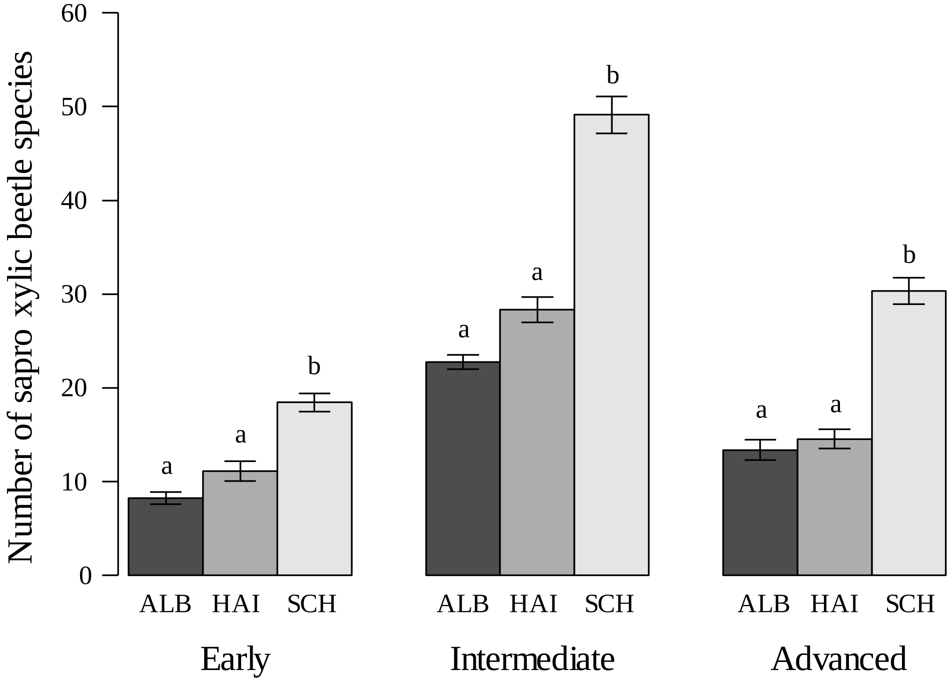


Fig. IV.1: Comparison of species richness of early, intermediate, advanced successional saproxylic beetles between the three study regions (ALB: Swabian Alb, HAI: Hainich-Dün, SCH: Schorfheide-Chorin). Mean values per region, error bars show S.E., different characters indicate significant differences.

Local stand factors

On local scale, plant diversity on the study sites negatively affected species richness of saproxylic beetles of each guild (Tab. IV.2; Fig. IV.2). Furthermore, species numbers in intermediate and advanced decayed wood increased with increasing diameter of trees on the study sites, whereas increasing deadwood amount negatively affected species richness in both guilds (Tab. IV.2; Appendix IV; Fig. IV.B3a-b). Increasing amounts of coniferous trees had positive effects on species numbers of saproxylic beetles of early and advanced decay stages (Tab.IV.2; Appendix IV.B, Fig. IV.B3c).

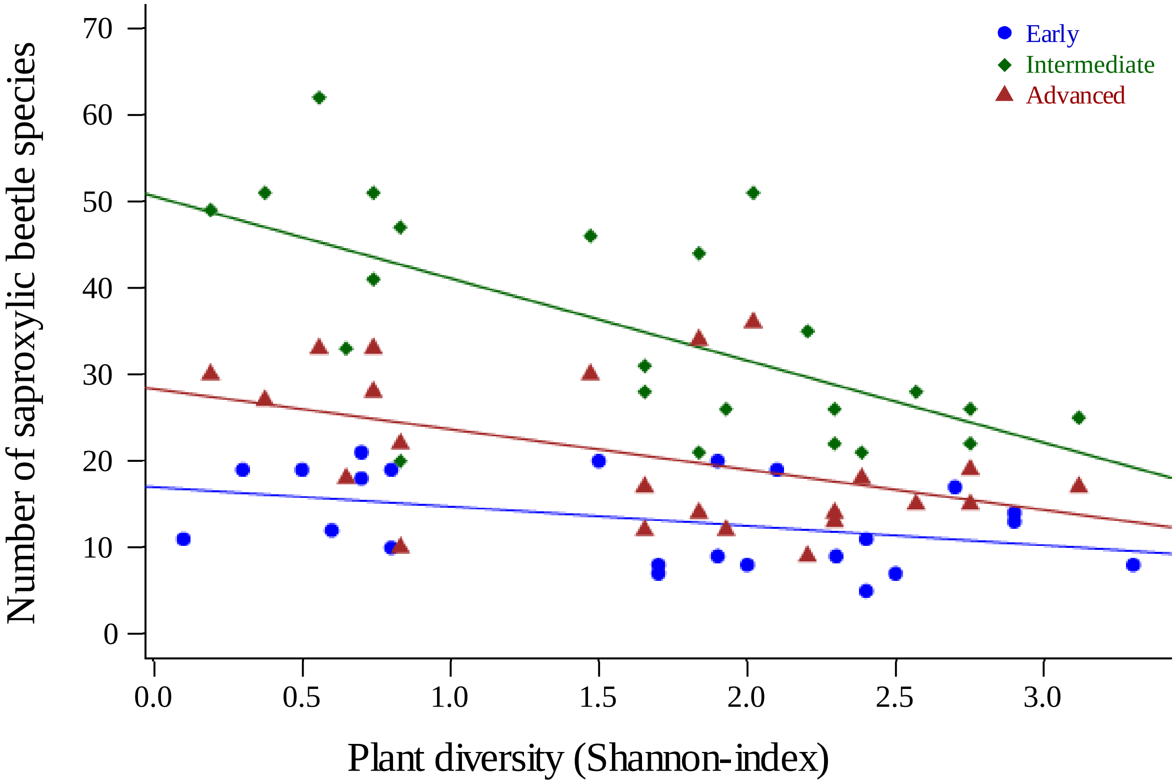


Fig. IV.2: Effects of plant diversity (Shannon-index) on species richness of early, intermediate, and advanced successional saproxylic beetles at local scale (r=0,1km). Significant correlations are indicated by solid lines.

Landscape composition

Increasing fragmentation of landscape at 2 km radius around the study sites adversely affected saproxylic species richness of early, intermediate and advanced decay stages (Tab. IV.2; Fig. IV.3). Moreover, with increasing forest area saproxylic beetle species richness of early and intermediate decay stages also increased (Appendix IV.B; Fig. IV.B4a). However, only saproxylic beetle species inhabiting early successional decay stages were positively affected by increasing amounts of arable land in the landscape (Appendix IV.B, Fig. IV.B4b).

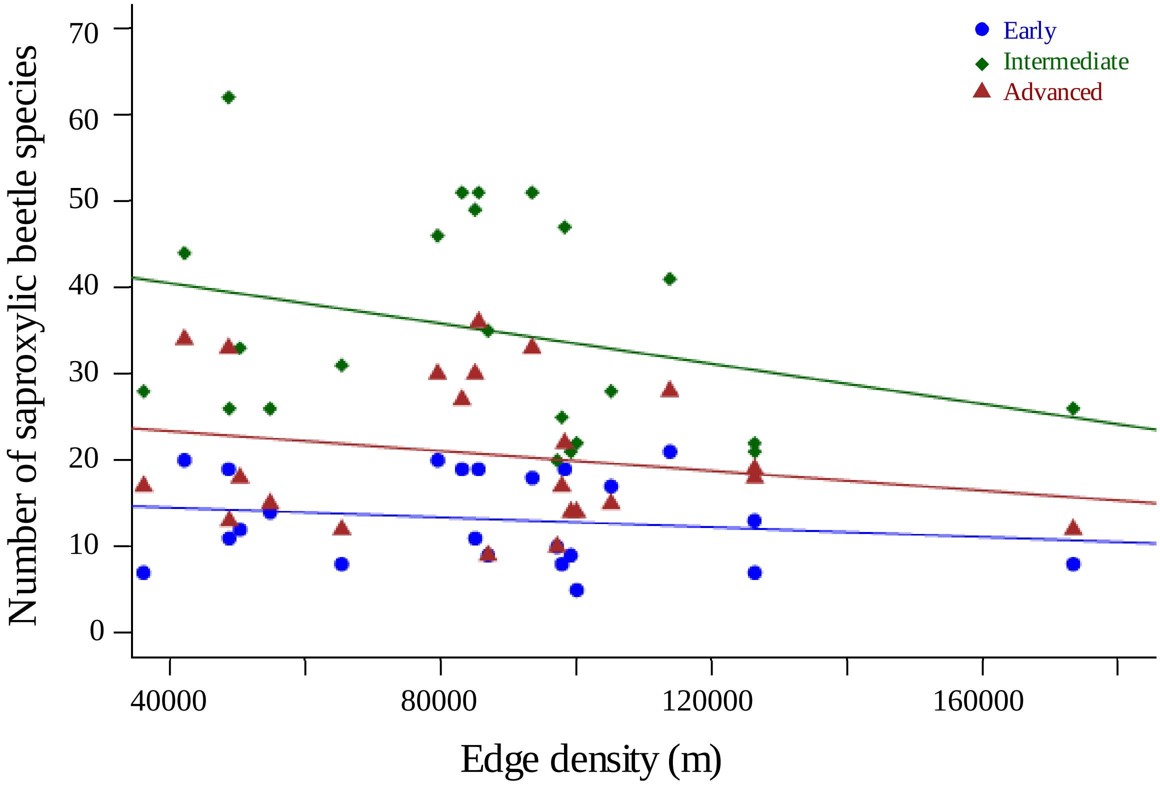


Fig. IV.3: Effects of fragmentation on species richness of early, intermediate, and advanced successional saproxylic beetles at landscape scale (r=2km). Significant correlations are indicated by solid lines.

Tab. IV.2: Linear mixed effect models of local stand factors, landscape features, and geographical conditions for species richness of saproxylic beetles inhabiting early, intermediate, and advanced decayed wood including all relevant covariates after model simplification. Significant factors are in bold.

		NumDF	DenDF	F-value	p-value
Early					
Local Stand Factors	**Proportion conifers**	**1**	**16**	**4.82**	**0.0433**
	Plant diversity	**1**	**16**	**22.72**	**0.0002**
	Tree cover	1	16	4.13	0.0592
	Tree diversity	1	16	1.08	0.3147
	Region	**2**	**16**	**24.47**	**<0.0001**
Landscape scale	**Area arable land**	**1**	**17**	**7.59**	**0.0135**
	Area forest	**1**	**17**	**6.74**	**0.0092**
	Edge density	**1**	**17**	**8.61**	**0.0188**
	Region	**1**	**17**	**30.19**	**<0.0001**
Regional scale	**Humidity**	**1**	**20**	**7.80**	**0.0112**
	Temperature	**1**	**20**	**11.54**	**0.0029**
Intermediate					
Local Stand Factors	**Deadwood amount**	**1**	**16**	**7.70**	**0.0135**
	DBH	**1**	**16**	**19.36**	**0.0004**
	Plant diversity	**1**	**16**	**59.07**	**<0.0001**
	Region	**2**	**16**	**24.09**	**<0.0001**
	Tree cover	1	16	3.84	0.0677
Landscape scale	**Area forest**	**1**	**17**	**10.44**	**0.0049**
	Area urban	1	17	3.36	0.0842
	Edge density	**1**	**17**	**10.84**	**0.0043**
	Region	**2**	**17**	**59.37**	**<0.0001**
Regional scale	**Humidity**	**1**	**20**	**14.60**	**0.0112**
	Temperature	**1**	**20**	**11.43**	**0.0029**
Advanced					
Local stand factors	**Deadwood amount**	**1**	**15**	**19.40**	**0.0005**
	DBH mean	**1**	**15**	**11.31**	**0.0043**
	Plant diversity	**1**	**15**	**35.10**	**<0.0001**
	Proportion conifer	**1**	**15**	**19.95**	**0.0005**
	Region	**2**	**15**	**23.19**	**<0.0001**
	Tree cover	**1**	**15**	**9.28**	**0.0082**

Tab. IV.2 continued

		NumDF	**DenDF**	**F-value**	**p-value**
Landscape scale	Area forest	1	18	0.09	0.7634
	Edge density	**1**	**18**	**6.71**	**0.0185**
	Region	**2**	**18**	**61.33**	**<0.0001**
Regional scale	**Humidity**	**1**	**20**	**14.52**	**0.0011**
	Temperature	**1**	**20**	**5.40**	**<0.0308**

Geographic conditions

Across the distinct regions, species richness of saproxylic beetles of three habitat guilds increased with warmer climatic conditions (Tab. IV.2; Fig. IV.4). However, humidity negatively affected species richness of early, intermediate, and advanced successional saproxylic beetles (Appendix IV.B, Fig. IV.B5).

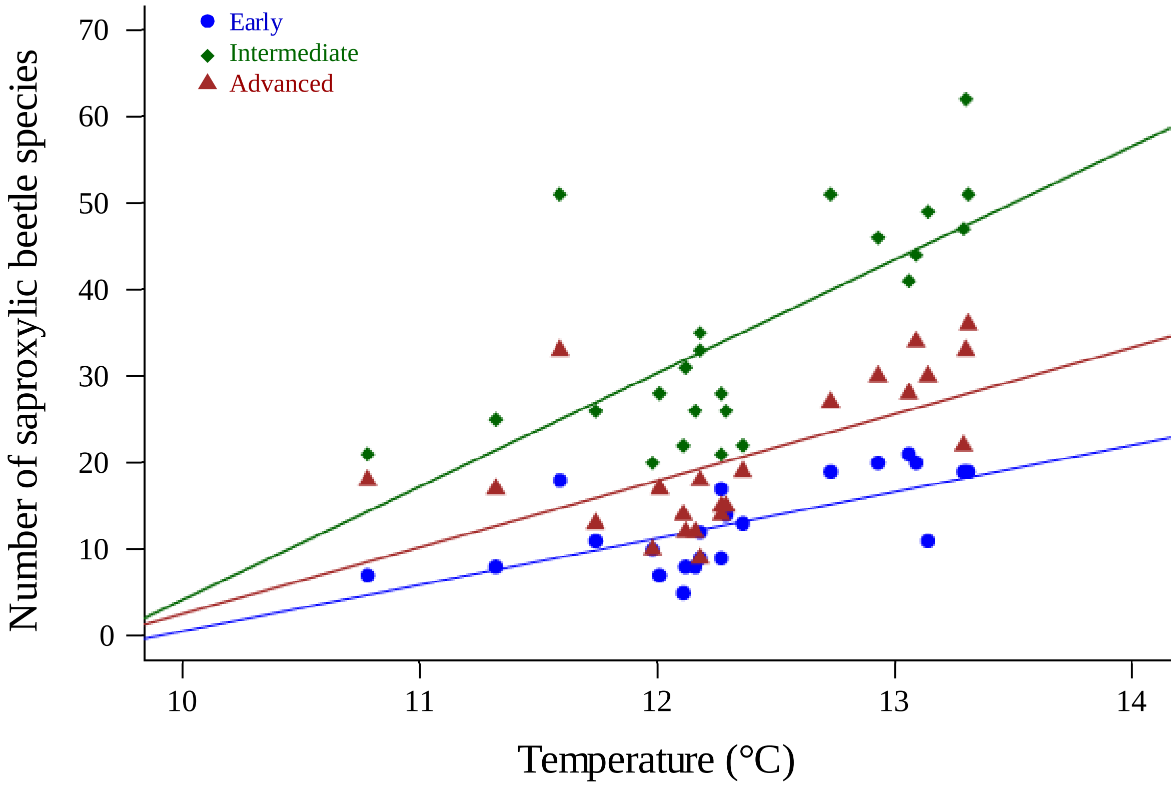


Fig. IV.4: Effects of annual mean temperature on species richness of early, intermediate, and advanced successional saproxylic beetles at regional scale. Significant correlations are indicated by solid lines.

Discussion

In this large-scale experiment we showed that environmental parameters on varying spatial scales affected saproxylic beetle guilds differently. Overall, increased fragmentation on local and landscape scale contributed to general decline of saproxylic species richness. Importantly, saproxylic species richness increased in warmer and less humid regions. Our results emphasize the need for guild-specific forest conservation schemes and deadwood management to maintain or even increase saproxylic beetle diversity in temperate forest ecosystems in central Europe.

Local stand factors

At local scale species richness of saproxylic beetles decreased with increasing plant diversity. Plant diversity is found to be highest along forest roads due to increased light conditions (Müller *et al.* 2008). Building of forest roads might disconnect meta-populations of saproxylic beetles, which put species with limited dispersal abilities to higher extinction risks (Ranius & Hedin 2001; Müller *et al.* 2005; Penttilä *et al.* 2006; Chiari *et al.* 2013). Furthermore, plant diversity was closely correlated to high amounts of understory. As beetles are ectothermic, their activity level depend on the temperature of the environment (Horák *et al.* 2012). Dense understory might lead to inhospitable microclimatic conditions of the downed exposed deadwood logs.

Increased diameter of living trees contributed to saproxylic diversity colonizing intermediate and advanced decay stages. Tree diameter is a measurement of tree height and thus tree age (Sumida *et al.* 2013). As described by the habitat-heterogeneity hypothesis, structurally complex old-grown trees provide key habitats for saproxylic beetles depending on intermediate and advanced successional deadwood structures, thereby maintaining species diversity (Jonsell *et al.* 1998; Ranius & Jansson 2000; Tews *et al.* 2004).

Interestingly, deadwood amount negatively affected saproxylic species richness inhabiting intermediate and advanced deadwood substrates. These findings could be explained by dilution effects of saproxylic beetles, due to locally higher availability of deadwood resources.

Our results indicate an increased species richness of early and late successional saproxylic beetle species in coniferous stands compared to deciduous forests. Light permeability is higher in conifer forests than in beech forests with dense leafy canopy. As insolation is one of the most important drivers of saproxylic beetle diversity conifer forests might provide more suitable habitat conditions (Hjältén *et al.* 2007; Johansson *et al.* 2007b; Vodka *et al.* 2008).

Landscape composition

In this study increasing edge density led to a general decline of saproxylic beetle species richness of all guilds. Similar to local fragmentation, disconnection of forest habitats at broader spatial scale prevent saproxylic beetle species dispersal (Ranius & Jansson 2000; Gibb *et al.* 2006a). As proposed by the meta-population concept long-term species persistence depends on emigration and immigration events (Hanski & Ovaskainen 2000; Ranius 2006). The fragmentation thresholds for successful individual migration within meta-populations are species-specific. Early successional saproxylic beetle species are able to overcome distances between 19 to 171 km, which might compensate the fragmentation effect to some extent (Nilssen 1984; Gibb *et al.* 2006a; Franc *et al.* 2007; Lassauce *et al.* 2011). This is partly reflected by our results as the slope for early successional beetles was relatively flat compared to intermediate and late successional beetles. However, saproxylic beetle species inhabiting advanced decayed deadwood structures often have limited dispersal abilities and remain in 250 to 1000 m distance to their larval habitat (Chiari *et al.* 2013). Accordingly, species richness of early and intermediate decay stages increased with higher proportions of forest area in the landscape. As recently shown, local species survival increased with habitat patch size (Ranius *et al.* 2014).

High proportions of arable land adjacent to forests promoted early successional saproxylic beetle diversity. Positive spill-over effects on species diversity are reported by agro-ecological studies when the adjacent habitats provided beneficial resources for the species (Steffan-Dewenter & Westphal 2007; Blitzer *et al.* 2012). Adults of many saproxylic beetle species, e.g. cerambycid species, depend on pollen or plant tissue provided by flowers. These species might benefit from adjacent cultivated land, where flowering plant resources are more available.

Geographic conditions

We found a strong relation to regional varying abiotic factors (temperature and humidity), which are denoted by a south-north gradient in Germany. Our results contributed to the species energy hypothesis (Wright 1983), which predicts higher species numbers under warmer climate conditions. As ectothermic organisms, beetles might do better at warmer forest sites, as shown for saproxylic indicator beetle species of montane forests (Lachat *et al.* 2012). However, species richness in all saproxylic guilds decreased with increased humidity. Through the bore holes water can penetrate the deadwood habitat which might led to unsuitable habitat conditions with rain falling often.

Schorfheide was found to be most species rich of saproxylic beetles, though forests in this region developed under anthropogenic influence. However, the admixture of birch and oak trees in this region might benefit saproxylic beetle species. Especially old-grown oak trees are known as keystone habitats and provide various deadwood structures (Franc *et al.* 2007; Lachat *et al.* 2012). Edge and spill-over effects between different forest types are known to enhance saproxylic diversity of early successional beetles due to their good dispersal abilities (Okland *et al.* 1996; Wermelinger *et al.* 2007), which might also be an explanation for the diverse beetle fauna in Schorfheide-Chorin (Wermelinger *et al.* 2007). Furthermore, the mean annual temperature in Schorfheide-Chorin is about 1 to 2°C higher compared to the other regions (Fischer *et al.* 2010). As shown for temperate saproxylic beetles large-scaled temperature differences are key factor in driving saproxylic beetle species richness and might even compensate less suitable habitat conditions on a local scale (Müller *et al.* 2014).

Conclusions

To preserve saproxylic beetle diversity the ongoing fragmentation of central European forests and surrounding landscapes must be reduced. Our large-scale experiment underlines the importance of landscape composition additional to local stand factors for high species diversity of saproxylic beetle guilds. To limit the decline of saproxylic beetle species, guild-specific environmental requirements should be implemented in sustainable management schemes. However, warm climate conditions might compensate effects of intensified forest management. Further studies are required to document the long-term dynamics of saproxylic beetle diversity in relation to environmental parameters on different spatial scales.

Appendix IV.A

Tab. IV.A.1: Variance Inflation Factor (VIF) of environmental variables at local, landscape, and regional scale.

	Environmental variables	Variance inflation factor (VIF)	
		All	Tested
Local stand factors	Deadwood Amount	1.983	1.798
	DBH	3.654	1.698
	Plant diversity	4.824	1.854
	Proportion Conifers	3.447	2.136
	Proportion Understory	9.653	---
	Stand density	5.094	---
	Tree Cover	4.320	2.403
	Tree diversity	1.734	1.548
Landscape scale	Area arable	1.702	1.320
	Area forest	1.614	1.503
	Area grassland	4.703	---
	Area nature reserve	2.080	1.935
	Area urban	1.587	1.566
	Area wetland	3.037	1.675
	Edge density	4.609	1.735
Regional scale	Altitude	73.111	---
	Humidity	47.831	1.538
	Temperature (10)	7.581	1.538

Tab. IV.A.2: Number of exposed deadwood logs and number and abundance of sampled saproxylic beetle species of the different habitat guilds within each study region.

Study Region	Exposed logs	All sampled beetles	Early successional beetles	Beetles of intermediate decay stages	Beetles of advanced decay stages
Swabian Alb	229	107 / 9,821	21 / 5,014	52 / 4,154	25 / 489
Hainich-Dün	229	143 / 15,614	27 / 10,308	66 / 4,215	34 / 863
Schorfheide-Chorin	230	264 / 12,395	45 / 5,873	119 / 3,050	65 / 2,857

Tab. IV.A.3: Classification of the sampled saproxylic beetle species into the different habitat guilds based on the calculated value of their habitat niche.

Beetle species	**Niche**	**Value**
Abraeus granulum	Advanced	4
Abraeus perpusillus	Advanced	4
Acalles camelus	Intermediate	3.25
Acalles hypocrita	Intermediate	3.25
Acritus minutus	Intermediate	2.25
Acrulia inflata	Advanced	3.67
Aeletes atomarius	Advanced	4
Agathidium nigripenne	Intermediate	3
Alosterna tabacicolor	Advanced	3.6
Ampedus balteatus	Intermediate	3.4
Ampedus cinnabarinus	Intermediate	3.4
Ampedus elongatulus	Advanced	3.67
Ampedus pomorum	Advanced	3.67
Ampedus rufipennis	Intermediate	3.4
Ampedus sanguineus	Intermediate	3.4
Anaglyptus mysticus	Intermediate	2.75
Anaspis flava	Advanced	4
Anaspis frontalis	Advanced	4
Anaspis lurida	Advanced	4
Anaspis regimbarti	Advanced	4
Anaspis ruficollis	Advanced	4
Anaspis rufilabris	Advanced	4
Anaspis thoracica	Advanced	4
Anisotoma castanea	Advanced	4
Anisotoma humeralis	Advanced	4
Anisotoma orbicularis	Advanced	4
Anobium costatum	Intermediate	2.5
Anobium pertinax	Intermediate	3
Anomognathus cuspidatus	Intermediate	2.75
Anthribus albinus	Intermediate	3
Aplocnemus impressus	Intermediate	3.25
Aplocnemus nigricornis	Intermediate	2.5
Arpidiphorus orbiculatus	Advanced	4
Atheta picipes	Intermediate	3.25
Atomaria bella	Intermediate	3
Atomaria ornata	Fresh	2
Atomaria procerula	Fresh	2
Atomaria turgida	Fresh	2
Atomaria umbrina	Fresh	2
Atrecus affinis	Advanced	4
Bibloporus bicolor	Intermediate	3.4
Bitoma crenata	Intermediate	2.5
Bolitochara lucida	Advanced	3.83
Bolitochara obliqua	Intermediate	3.25
Bolitophagus reticulatus	Intermediate	3.33
Caenoscelis ferruginea	Advanced	4
Cerylon fagi	Advanced	3.67
Cerylon ferrugineum	Intermediate	2.4
Cerylon histeroides	Advanced	3.67
Cetonia aurata	Advanced	4
Choragus sheppardi	Intermediate	3
Cis boleti	Intermediate	3.4
Cis dentatus	Intermediate	3.25
Cis glabratus	Intermediate	3.25
Cis hispidus	Intermediate	3.25
Cis jacquemartii	Intermediate	3.25
Cis micans	Intermediate	3.25
Cis nitidus	Intermediate	3.4
Cis punctulatus	Intermediate	3.25
Cis rugulosus	Intermediate	3.25
Cis setiger	Intermediate	3.25
Corticaria abietorum	Intermediate	2.25
Corticaria linearis	Intermediate	2.25
Corticaria longicollis	Advanced	4.29
Corticarina lambiana	Intermediate	2.5
Corticeus unicolor	Intermediate	2.5
Corymbia rubra	Advanced	3.5
Corymbia scutellata	Intermediate	3.4
Cryphalus abietis	Fresh	2
Crypturgus hispidulus	Fresh	2
Crypturgus pusillus	Fresh	2
Cychramus variegatus	Intermediate	3.4
Dacne bipustulata	Intermediate	3.17
Dadobia immersa	Intermediate	2.5
Dasytes aeratus	Intermediate	3.2
Dasytes plumbeus	Intermediate	3.2
Denticollis linearis	Intermediate	3.4
Denticollis rubens	Intermediate	3.4

Beetle species	**Niche**	**Value**	**Beetle species**	**Niche**	**Value**
Dinaraea aequata	Advanced	3.5	*Hylis olexai*	Advanced	3.5
Diplocoelus fagi	Intermediate	2.5	*Hylobius abietis*	Fresh	2
Dissoleucas niveirostris	Intermediate	3	*Hylurgops palliatus*	Fresh	2
Dorcus parallelipipedus	Intermediate	3.4	*Ischnoglossa prolixa*	Intermediate	3.25
Dryocoetes autographus	Fresh	2	*Ischnomera cyanea*	Intermediate	3.4
Dryocoetes villosus	Fresh	2	*Laemophloeus monilis*	Intermediate	2.5
Endomychus coccineus	Intermediate	3.4	*Latridius consimilis*	Advanced	3.71
Enicmus atriceps	Intermediate	3	*Latridius hirtus*	Advanced	4
Enicmus brevicornis	Intermediate	2.5	*Leiopus nebulosus*	Fresh	2
Enicmus fungicola	Advanced	3.75	*Leperisinus fraxini*	Fresh	2
Enicmus planipennis	Advanced	3.5	*Leptura quadrifasciata*	Intermediate	3.25
Enicmus testaceus	Intermediate	3	*Leptusa fumida*	Advanced	3.8
Ennearthron cornutum	Intermediate	3.4	*Leptusa pulchella*	Advanced	3.8
Epuraea longula	Fresh	1.6	*Litargus connexus*	Intermediate	2.75
Epuraea marseuli	Intermediate	2.25	*Malachius bipustulatus*	Intermediate	3.2
Epuraea neglecta	Fresh	1.6	*Malthinus facialis*	Intermediate	3.2
Epuraea pygmaea	Advanced	4	*Malthinus punctatus*	Intermediate	3.2
Epuraea variegata	Intermediate	3.4	*Malthodes crassicornis*	Intermediate	3.2
Ernobius mollis	Intermediate	2.5	*Malthodes guttifer*	Intermediate	3.2
Ernobius nigrinus	Fresh	1.86	*Malthodes marginatus*	Intermediate	3.2
Ernoporicus fagi	Fresh	2	*Malthodes pumilus*	Intermediate	3.2
Euplectus fauveli	Advanced	4.33	*Malthodes spathifer*	Intermediate	3.2
Euplectus karsteni	Advanced	4.13	*Megatoma undata*	Advanced	3.5
Euplectus nanus	Advanced	4	*Melandrya barbata*	Intermediate	3.4
Euryusa castanoptera	Fresh	2	*Melandrya caraboides*	Intermediate	3.4
Gabrius splendidulus	Advanced	3.71	*Melanotus castanipes*	Advanced	3.67
Glischrochilus quadripunctatus	Fresh	2	*Melanotus rufipes*	Advanced	3.67
Globicornis corticalis	Advanced	3.5	*Melasis buprestoides*	Intermediate	3
Gyrophaena boleti	Intermediate	3.25	*Micrambe abietis*	Fresh	2
Gyrophaena minima	Advanced	3.67	*Micridium halidaii*	Advanced	4.4
Hedobia imperialis	Intermediate	3	*Microscydmus minimus*	Advanced	4.5
Hololepta plana	Intermediate	2.4	*Mycetina cruciata*	Advanced	3.5
Hylastes attenuatus	Fresh	2	*Mycetophagus atomarius*	Intermediate	3.17
Hylecoetus dermestoides	Fresh	2	*Mycetophagus fulvicollis*	Advanced	3.8
Hylesinus crenatus	Fresh	2	*Mycetophagus quadripustulatus*	Intermediate	3.4
Hylis cariniceps	Advanced	3.5	*Nemadus colonoides*	Advanced	4.75
Hylis foveicollis	Advanced	3.5	*Nemosoma elongatum*	Fresh	2

Beetle species	**Niche**	**Value**	**Beetle species**	**Niche**	**Value**
Neuraphes carinatus	Advanced	3.89	*Plegaderus caesus*	Advanced	4
Neuraphes plicicollis	Advanced	4	*Plegaderus dissectus*	Advanced	4
Nosodendron fasciculare	Fresh	1.5	*Plegaderus vulneratus*	Fresh	2
Nudobius lentus	Intermediate	2.25	*Pogonocherus fasciculatus*	Intermediate	2.25
Obrium brunneum	Fresh	2	*Pogonocherus hispidulus*	Intermediate	2.25
Octotemnus glabriculus	Intermediate	3.4	*Prionocyphon serricornis*	Intermediate	3
Opilo mollis	Intermediate	3	*Prionychus ater*	Advanced	4.6
Orchesia micans	Intermediate	3.25	*Ptenidium gressneri*	Advanced	4.5
Orchesia minor	Intermediate	3.4	*Pteryx suturalis*	Advanced	4.13
Orchesia undulata	Advanced	3.5	*Ptilinus pectinicornis*	Intermediate	3
Orthocis alni	Intermediate	2.75	*Ptinella aptera*	Advanced	4
Orthocis festivus	Intermediate	3	*Ptinella limbata*	Advanced	4
Orthoperus atomus	Intermediate	3.29	*Ptinella tenella*	Advanced	4
Orthoperus mundus	Intermediate	3.29	*Pyrochroa coccinea*	Intermediate	2.4
Orthoperus nigrescens	Intermediate	3.29	*Pyrrhidium sanguineum*	Fresh	2
Orthotomicus laricis	Fresh	2	*Quedius maurus*	Advanced	4.6
Pachytodes cerambyciformis	Intermediate	3.17	*Quedius xanthopus*	Advanced	3.67
Paromalus flavicornis	Intermediate	3.43	*Rabocerus foveolatus*	Fresh	2
Paromalus parallelepipedus	Fresh	2	*Rhagium bifasciatum*	Intermediate	3.4
Pediacus depressus	Fresh	2	*Rhagium inquisitor*	Intermediate	2.4
Phloeocharis subtilissima	Intermediate	3	*Rhagium mordax*	Intermediate	2.25
Phloeonomus punctipennis	Intermediate	2.5	*Rhizophagus bipustulatus*	Intermediate	2.5
Phloeopora corticalis	Intermediate	2.25	*Rhizophagus cribratus*	Intermediate	2.71
Phloeopora testacea	Intermediate	2.25	*Rhizophagus depressus*	Fresh	2
Pityophagus ferrugineus	Fresh	2	*Rhizophagus dispar*	Intermediate	2.5
Pityophthorus lichtensteini	Fresh	2	*Rhizophagus ferrugineus*	Fresh	2
Pityophthorus pityographus	Fresh	1.75	*Rhizophagus nitidulus*	Intermediate	2.8
Pityophthorus pubescens	Fresh	2	*Rhizophagus parvulus*	Fresh	1.6
Placonotus testaceus	Intermediate	2.5	*Rhizophagus perforatus*	Fresh	2
Placusa tachyporoides	Fresh	1.6	*Rhizophagus picipes*	Intermediate	2.25
Platycerus caraboides	Intermediate	3.4	*Rhyncolus ater*	Intermediate	3
Platydema violaceum	Intermediate	3.4	*Rhyncolus elongatus*	Intermediate	3
Platyrhinus resinosus	Intermediate	3	*Rhyncolus sculpturatus*	Intermediate	3
Platysoma compressum	Intermediate	2.4	*Salpingus planirostris*	Intermediate	2.25
Plectophloeus fischeri	Advanced	4.17	*Salpingus ruficollis*	Intermediate	2.25

Beetle species	**Niche**	**Value**
Saperda scalaris	Fresh	2
Scaphidium quadrimaculatum	Advanced	4
Schizotus pectinicornis	Intermediate	2.5
Scolytus intricatus	Fresh	1.75
Sepedophilus testaceus	Advanced	4.13
Silvanus bidentatus	Fresh	2
Silvanus unidentatus	Fresh	2
Sinodendron cylindricum	Intermediate	3.25
Sphaeriestes castaneus	Fresh	2
Sphindus dubius	Advanced	4
Stenagostus rhombeus	Intermediate	3.4
Stenichnus bicolor	Intermediate	3.17
Stenichnus godarti	Advanced	4
Stenostola dubia	Intermediate	3
Stephostethus alternans	Intermediate	3
Stephostethus rugicollis	Intermediate	2.5
Stereocorynes truncorum	Intermediate	3
Sulcacis affinis	Intermediate	3.4
Sulcacis fronticornis	Intermediate	3.4
Synchita humeralis	Intermediate	3.25
Tachyta nana	Intermediate	2.83
Taphrorychus bicolor	Fresh	2
Thanasimus formicarius	Intermediate	2.25
Tillus elongatus	Intermediate	3
Tomoxia bucephala	Intermediate	3
Trachodes hispidus	Advanced	3.5
Triphyllus bicolor	Advanced	3.5
Triplax aenea	Intermediate	3.4
Triplax russica	Intermediate	3.4
Tritoma bipustulata	Intermediate	3.4
Tropideres albirostris	Intermediate	2.25
Uleiota planata	Intermediate	2.5
Uloma culinaris	Intermediate	3.4
Variimorda fasciata	Intermediate	3
Vincenzellus ruficollis	Intermediate	2.4
Xestobium plumbeum	Intermediate	2.5
Xyleborus dispar	Fresh	2
Xyleborus germanus	Fresh	2
Xyleborus monographus	Fresh	2
Xyleborus saxeseni	Fresh	2
Xylita laevigata	Advanced	3.5
Xyloterus domesticus	Fresh	2
Xyloterus lineatus	Fresh	2
Xyloterus signatus	Fresh	2

Appendix IV.B

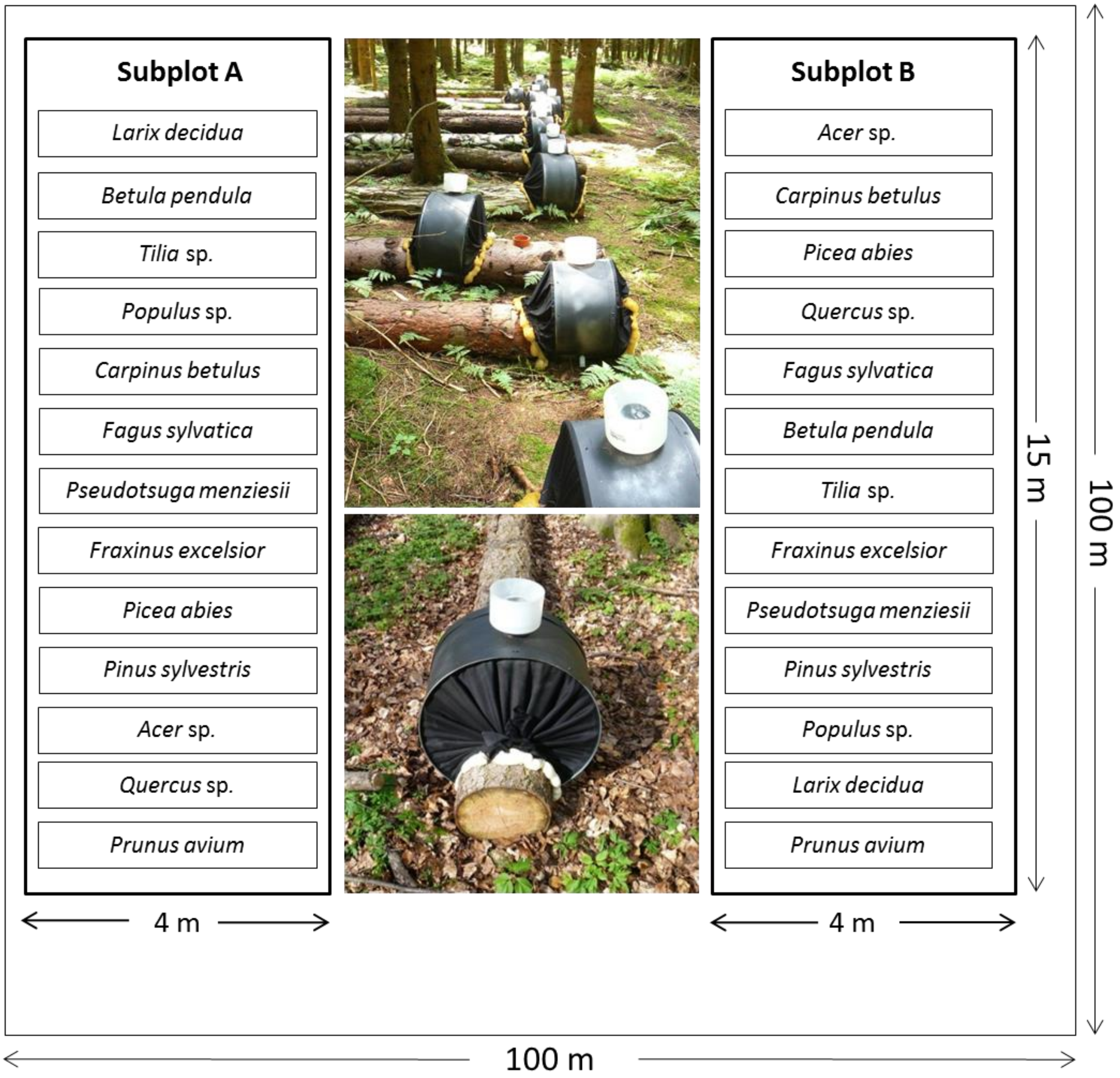
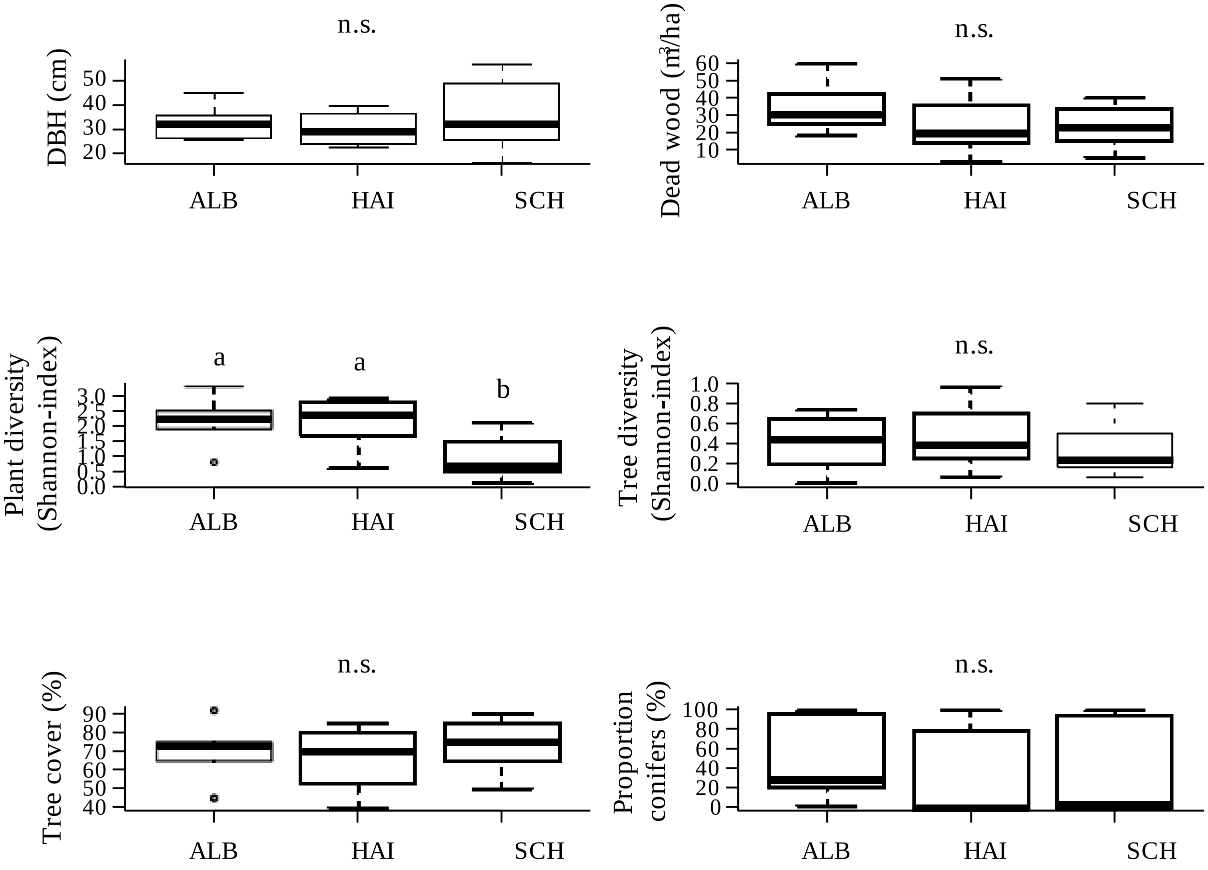


Fig. IV.B.1: General study design.

a)


n.s.
DBH (cm)
50
40
30
20
ALB
HAI
SCH
n.s.
Dead wood (m³/ha)
60
50
40
30
20
10
ALB
HAI
SCH
a
a
b
Plant diversity (Shannon-index)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
ALB
HAI
SCH
n.s.
Tree diversity (Shannon-index)
1.0
0.8
0.6
0.4
0.2
0.0
ALB
HAI
SCH
n.s.
Tree cover (%)
90
80
70
60
50
40
ALB
HAI
SCH
n.s.
Proportion conifers (%)
100
80
60
40
20
0
ALB
HAI
SCH

b)

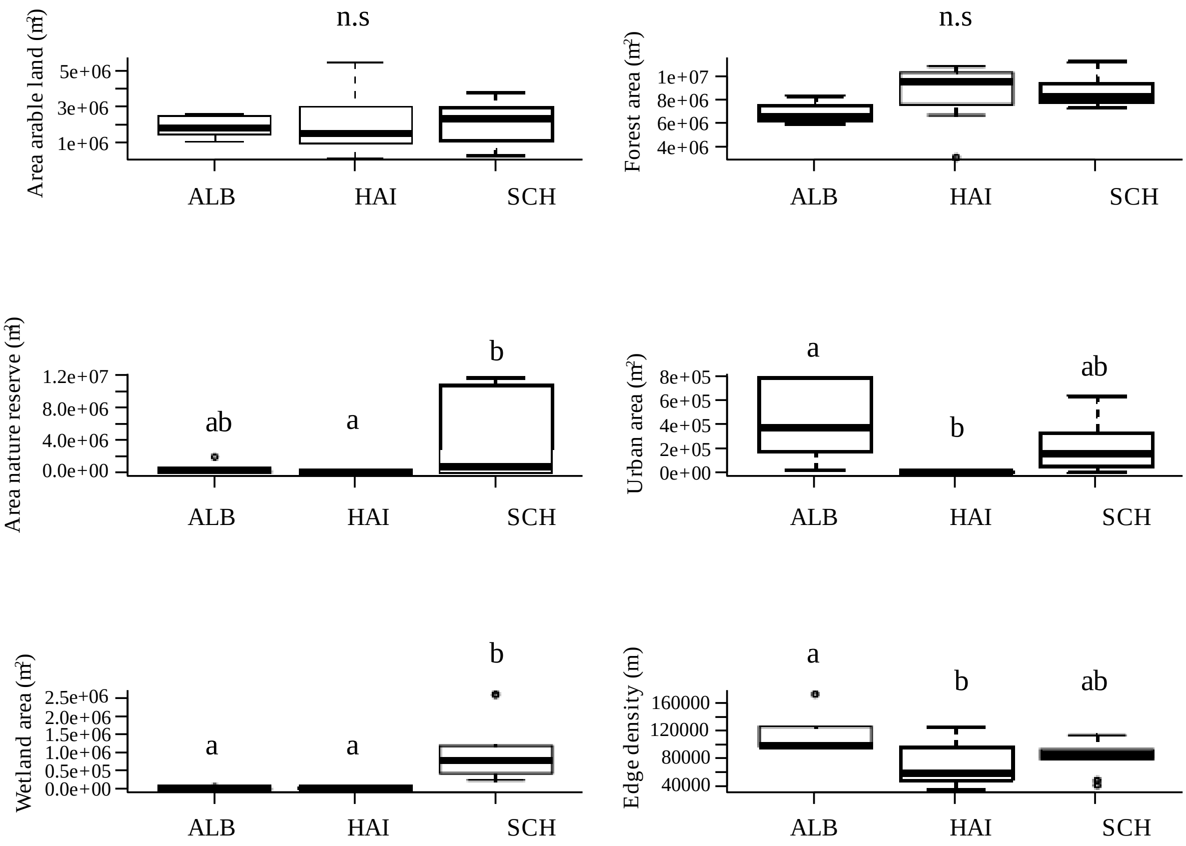


Fig. IV.B.2: Comparison of a) local stand factors and b) parameters on landscape scale between the study regions (ALB: Swabian Alb, HAI: Hainich-Dün, SCH: Schorfheide-Chorin). Mean values per region, error bars show S.E., different characters indicate significant differences. Non-significance is indicated by n.s.

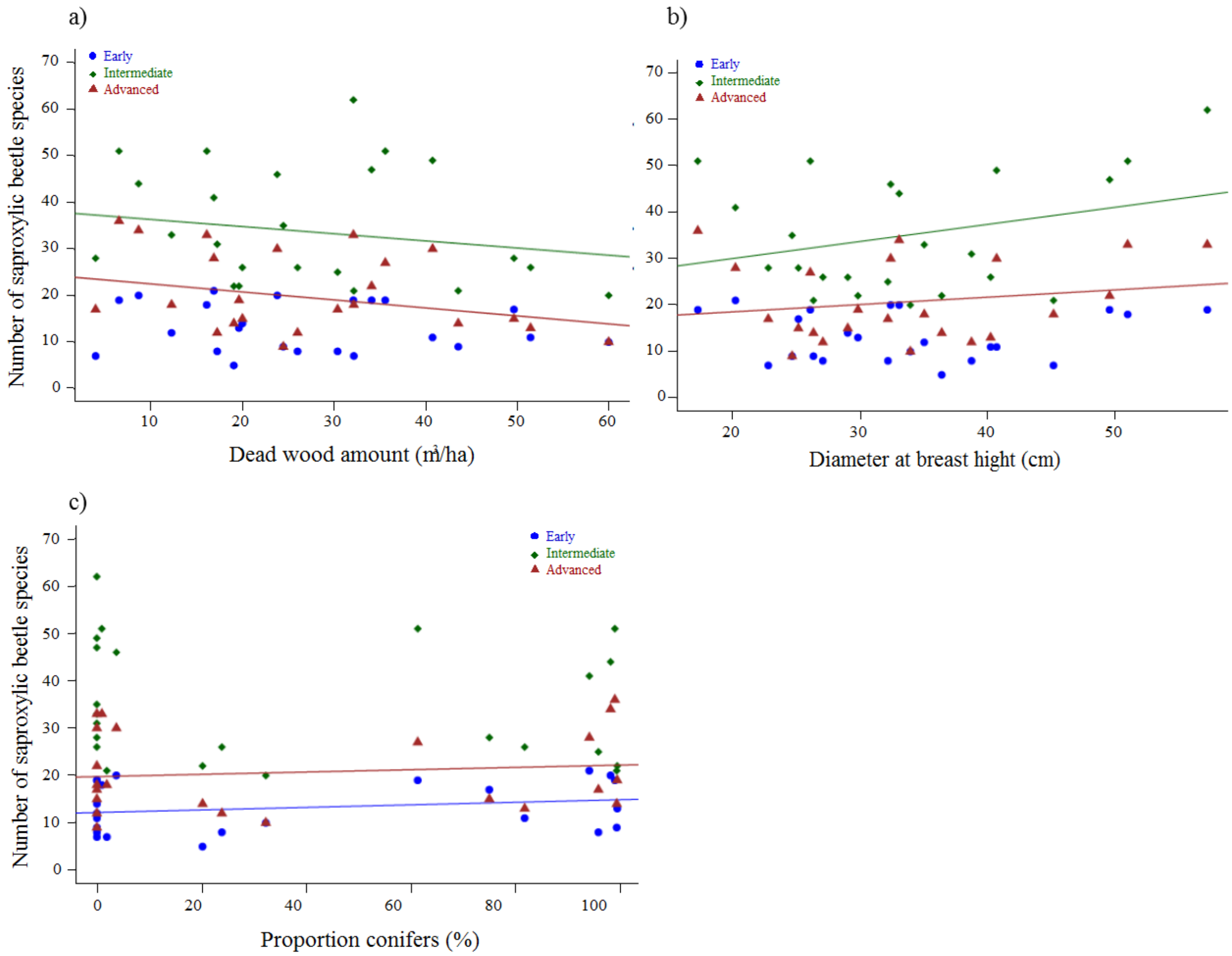


Fig. IV.B.3: Effects of the local stand factors a) deadwood amount (m^3/ha), b) DBH (cm), and c) proportion of conifers on species richness of early, intermediate, and advanced successional saproxylic beetles. Significant correlations are indicated by solid lines.

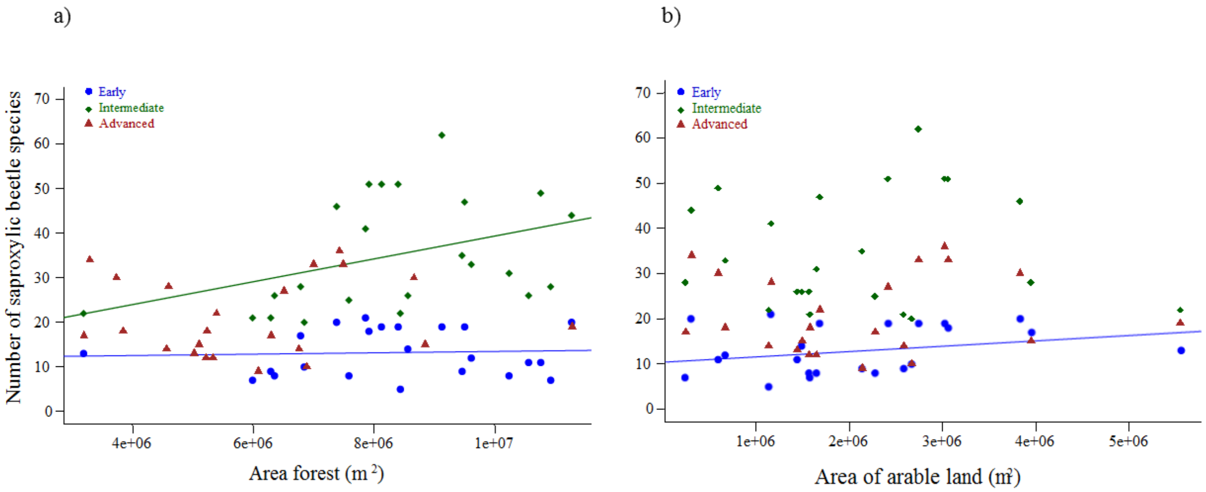


Fig. IV.B.4: Effects of a) forest area (m^2) and b) area of arable land (m^2) measured at 2 km radius around the study sites on species richness of early, intermediate, and advanced successional saproxylic beetles. Significant correlations are indicated by solid lines.

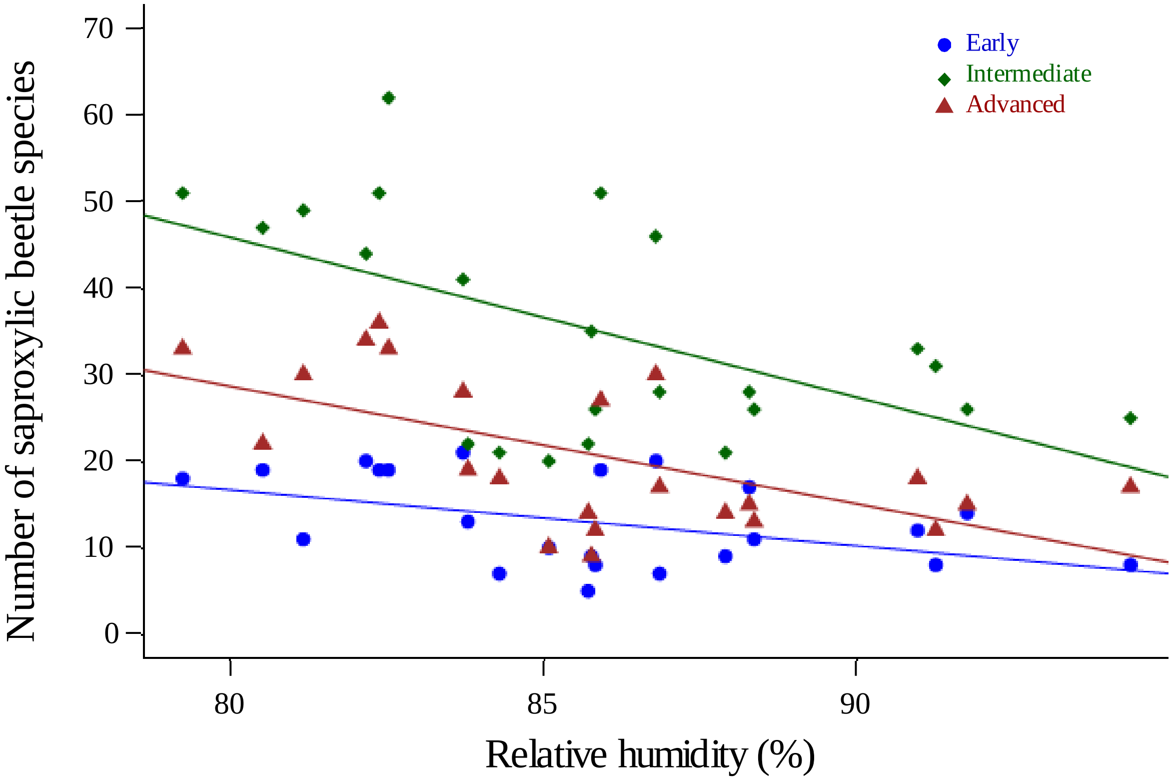


Fig. IV.B.5: Effects of relative humidity (%) on species richness of early, intermediate, and advanced successional saproxylic beetles. Significant correlations are indicated by solid lines.

CHAPTER V: GENERAL DISCUSSION

The high productivity of forest ecosystems is based on the decomposition of organic matter which converts forest floor into fertile soils. However, the intensification of forest management has caused dearth of dead organic material, e.g. large diameter deadwood, and consequently rapid declines of associated saproxylic beetle species. Therefore, the long-term and large-scale research project BELONGDEAD aims to investigate the interplay of saproxylic biodiversity and decomposition, and the effects of forestry intensity on both. Decomposition rates and residence time of deadwood depend on the activity of associated detrivores and decomposers. Deadwood hosting high densities of saproxylic species and individuals is supposed to decompose faster. Diversity patterns of saproxylic organisms directly provide information how long deadwood items might reside in forest ecosystems, thereby allowing conclusions to be drawn about the future carbon stocks of forests (Russell *et al.* 2014). In the framework of the BeLongDead-project my dissertation focussed on the first steps of deadwood decomposition of 13 tree species by analysing diversity of saproxylic beetles hatching of experimentally exposed fresh deadwood logs in differently managed forests in 3 study regions across Germany.

Tree species identity determined interaction patterns of saproxylic beetles

Tree species identity of the exposed logs was an important driver of saproxylic beetle diversity and abundance (chapter II). Especially for wood-dependent xylophagous beetles tree species identity of deadwood items were crucial, as most members of this guild revealed to be resource specialists compared to saproxylic fungivores and predators (chapter III).

A successful colonization and resource exploitation by saproxylic beetles depends on the quality of the resource to meet the species specific requirements. Wood of each tree species has its specific structural and chemical properties, e.g. thickness and structure of the bark, moisture, lignin, and tannin content, as well as mineral inclusions of the wood, thus creating different habitat niches. These specific characteristics are still present in fresh deadwood, thus species colonization patterns of early successional saproxylic beetles are driven by tree species identity (Cornwell *et al.* 2009; Fontaine *et al.* 2009). Moreover, as shown for herbivores, specialists which have adapted to specific characteristics and developed strategies to overcome poisonous effects of the chemical compounds in plant material have vital advantages over generalists (Brandle & Brandl 2001; Montoya *et al.* 2006). Accordingly, networks of saproxylic beetles feeding directly on wood were more specialized than saproxylic networks of mycetophagous and predatory beetles (chapter III).

However, strictly speaking the latter explains why certain species preferably inhabit deadwood of a specific tree species but not why some tree species are colonized by many beetle species and some are colonized by only a few. An explanation of species richness patterns on host plants is suggested by the species area hypothesis that phytophagous species numbers and abundance are positively correlated to abundance and distribution of their host trees (Bussler *et al.* 2011). Depending on region and management type dominant tree species at the forest sites were either, *Picea abies, Pinus sylvestris,* or *Fagus sylvatica*. Thus, these tree species should have hosted highest saproxylic species numbers. However, consistent for all regions, only about 50% of the sampled saproxylic species were found on logs of *P. abies, P. sylvestris,* and *F. sylvatica*, whereas logs of *Carpinus betulus, Prunus avium,* and *Acer sp*. hosted region-specific most species. This result might be attributed to dilution as well as concentration effects. Dilution effects might occur by high resource availability (here: deadwood of *P. abies, P. sylvestris,* and *F. sylvatica*) within the dispersal range of their potential inhabitants; conversely, if the resource is only poorly represented (here deadwood of *C. betulus, Prunus avium*) then species and specimen might be found in high densities on only few items. Moreover, we found no effect of the available deadwood amount of the forest sites on local species richness (chapter IV), which might contribute to the dilution hypothesis. Furthermore, especially early successional beetles are good disperses, which are able to overcome even distances of about 170 km (Nilssen 1984). To investigate dilution effects, not the deadwood amount and distribution at local but on landscape or even regional scale might be decisive for beetle species colonizing fresh deadwood.

Decay rates of deadwood are species-specific. Thus, resource quality and condition offered by deadwood differ between tree species. Conifers are known to decay more slowly than deciduous tree species (Thomas *et al.* 2009; Russell *et al.* 2014). However, *C. betulus* logs decay fast and provide various microhabitats simultaneously for early and later successional saproxylic beetle species, which might explain high beetle species numbers.

Forest management effects on saproxylic beetle species richness

Contrary to our expectations intensively managed conifer forests revealed to be species rich and hosted diverse communities, resulting in more robust network structure compared to managed and unmanaged beech forests (chapters II and III). How can this result be explained when studies concerning saproxylic species richness and forest management often found higher species diversity the more natural the investigated forests (Bengtsson *et al.* 2000; Grove 2002a; Johansson *et al.* 2007b; Djupström *et al.* 2008; Brunet & Isacsson 2009; Paillet *et al.* 2010)?

Generally, it is crucial to keep in mind that we investigated fresh deadwood, and most saproxylic beetle species sampled belonged to the guild of early successional beetles. Thus, the better asked questions are, firstly, which factors promote species diversity of early successional saproxylic beetles and, secondly, in how meet conifer forests the demands of this saproxylic beetle guild better than the managed and unmanaged beech forests?

In respect to the first question, most essential for early successional saproxylics is a fair supply of freshly logged wood or deadwood in early decay stages. Although managed (conifer and beech) forests temporarily offer quite high amounts of freshly logged deadwood due to logging events, the cut logs are quickly transferred to timber-processing companies. However, living spruce and pine trees often develop dead and dying branches, which might serve as saproxylic habitats in conifer forests. The investigated managed beech forests sites are currently in their medium age (Fischer *et al.* 2010). However, in beech forests, naturally occurring deadwood follows an U-shaped curve over time, with lowest amounts in medium age (Holzwarth *et al.* 2013). The unmanaged beech forest sites investigated were taken out of management 10 to 30 years ago. The time needed to re-establish the conditions of species rich old-growth forests with high amounts of deadwood is assumed to be 270 to 300 years (Hörnberg *et al.* 1998). Contributing to this, it has been shown that managed forests outnumber set-aside forests in terms of species richness within the first 20 years after abandonment of management practices (Paillet *et al.* 2010).

With regard to the second question, one of the most important drivers of saproxylic diversity found in European forests is insolation (Kaila *et al.* 1997; Jonsell *et al.* 1998; Ranius & Jansson 2000; Kappes & Topp 2004; Saint-Germain *et al.* 2004; Lindhe *et al.* 2005; Horák *et al.* 2012; Koch Widerberg *et al.* 2012). In the past, European forests were characterized by a semi-open structure with openings and gaps due to the activities, first of mega-herbivores, later of domestic mammal grazers (Bengtsson *et al.* 2000). Moreover, local disturbances (fires, storms, etc.) created large amounts of sun-exposed deadwood (Djupström *et al.* 2012). Saproxylic species have evolved in response to these conditions, which explains the importance of sun-exposed deadwood for saproxylic beetle diversity (Bengtsson *et al.* 2000). Today, a high light permeability is characteristic of conifer forests, thereby reflecting past habitat conditions; whereas in beech forests the foliage leaves most parts of the forest floor and, thus, downed deadwood shaded.

Regional differences in saproxylic beetle diversity and specialisation

Hotspots of biodiversity are places where most endemic species found suitable conditions for feeding and breeding in a temporal and spatial context respectively, i.e. the number of available ecological niches is high (Myers *et al.* 2000; Vodka *et al.* 2008). Known biodiversity hotspots are old-grown beech forests which might exclusively be found in the Hainich-Dün region (Müller *et al.* 2007; Sobek *et al.* 2009). Thus, we expected highest saproxylic beetle species richness in this region. However, the most diverse saproxylic community was found in Schorfheide-Chorin compared to the other study regions though forests in this region developed under anthropogenic influence (chapter II). Forest area in Schorfheide-Chorin consists of a mosaic of traditional oak and beech forests, alder-marsh forests and intensively managed pine forests (www.biodiversity-exploratories.de). The intermediate-disturbance hypothesis of Connell (1978) postulates higher species diversity in regions with intermediate levels of disturbance, which creates a balanced frequency of different habitat types. Edge and spill-over effects between the various forest types might contribute to the high species diversity (Okland *et al.* 1996; Wermelinger *et al.* 2007). Until recently, most forests in Schorfheide-Chorin served as state hunting areas. The game wild kept the understory and the amount of young trees at low levels, which allowed the development of single standing old-grown oak trees. Oaks are important keystone habitats of saproxylic beetles due to various deadwood structures provided at old age (Franc *et al.* 2007; Lachat *et al.* 2012).

Hence, we sampled highest species richness in Schorfheide; specialisation degree was highest for the investigated trophic guilds in Hainich-Dün (chapter III). Sahlin & Schroeder

(2009) suggested that specialized herbivores reach higher densities in larger areas due to high immigration rates. Hainich-Dün comprises the largest connected forest area in Germany (Sobek *et al.* 2009), thus our findings can be attributed to the proposed resource-concentration hypothesis. Moreover, it underlines the importance of habitat connection of old-grown forests as refuge area for saproxylic specialists. As recently shown, local species survival increased with patch size of the habitat (Ranius *et al.* 2014).

Environmental factors important for saproxylic beetle guilds at different spatial scales

The reduction of deadwood quantity and quality on local scale is considered main reason for the rapid decline of saproxylic beetle species. However, the importance of forest landscape composition and regional varying abiotic conditions on saproxylic beetle guilds remained largely untested (Gibb *et al.* 2006a; Franc *et al.* 2007). In chapter IV, we investigated the relationship of 13 environmental factors on diversity of early, intermediate and late successional saproxylic beetles at three spatial scales (local stand factors at 0.1 km radius around the study plots, landscape composition at 2 km radius around the study plots, and abiotic conditions in 400 km to 700 km distance). Increased fragmentation at local and landscape scale negatively affected species richness of saproxylic beetle guilds (chapter IV). Basis for the continued existence of meta-populations are emigration and immigration events (Hanski & Ovaskainen 2000; Ranius 2006). If the distance between the spatially separated populations becomes too far to overcome, local species extinctions might occur. However, dispersal abilities are species-specific. Early successional beetles might be able to compensate increased habitat fragmentation to some extent, as most members of this guild are able to disperse over large distances (Nilssen 1984; Gibb *et al.* 2006a; Franc *et al.* 2007; Lassauce *et al.* 2011). Accordingly, the fragmentation effect was more pronounced for intermediate and late successional beetle species, which often have limited dispersal abilities (Chiari *et al.* 2013).

Temperature and humidity were strong predictors of saproxylic beetle species richness (chapter IV). According to the species energy hypothesis (Wright 1983), increased annual mean temperature contributed to overall saproxylic species richness. Beetles are ectothermic organisms, thus, their activity level depend on the temperature of their environment (Horák *et al.* 2012). Increased humidity negatively affected species richness of saproxylic guilds.

Deadwood is an important reservoir for water as it can easily penetrate the wood through the bore holes of the beetles. However, increased rainfall events might lead to unsuitable habitat conditions in the deadwood for saproxylic beetles.

Conclusions

To reduce the still ongoing decline of saproxylic forest biota, thereby securing the stability of forest ecosystems and its functions, but also meeting the demands of the woody industry and the needs for renewable resources are most central issues for sustainable forestry (Bellassen & Luyssaert 2014). A promising conservation method is the identification of a specific tree species and accumulation its deadwood, which might serve as an umbrella for high saproxylic diversity (Müller *et al.* (2012).

However, by investigating deadwood of 13 tree species, we proofed that not a single tree species but a mixture is necessary to preserve saproxylic beetle diversity. Moreover, the importance of specific tree species identity for saproxylic colonization behaviour was regionally different. The analyses of the interaction networks of different saproxylic beetle guilds revealed that especially primary colonizers, which initialise the decomposition process are highly specialised in terms of tree species identity of the deadwood items. Interaction frequency was highest for deadwood of *P. abies*. As *P. abies* is one of the most dominant tree species in European forests one might expect no endangerment for saproxylic beetles depending on spruce as resource. However, under the aspect of climate change, simulations of climate envelopes are indicating that *P. abies* will not be able to cope with higher mean temperatures in Central Europe (Thomas *et al.* 2004; Kölling 2007; Jandl *et al.* 2012). Therefore, dramatic losses of distribution area and abundance of *P. abies* will be the consequence, accompanied by decline of the associated saproxylic beetle fauna. More importantly, the specific ecosystem functions fulfilled by spruce specialists, which other species could not be take over, will also be lost.

To put it in a nutshell, in this dissertation I was able to identify main drivers of saproxylic beetle species preferably colonizing early successional deadwood via a large-scale experiment. For maintenance of saproxylic beetle diversity and their specific ecosystem functions modern I suggest that modern forestry should aim on (i) the promotion a mixed tree species composition under consideration of regional differences; (ii) the allowance for trees to grow old and the development of natural deadwood, which includes non-removal of senescent trees and standing deadwood; (iii) management practices that support a multi-layered forest structure with sun-exposed as well as shaded habitat conditions.

Outlook

One have to keep in mind that this dissertation focussed on the first steps of deadwood decomposition, and drawing the conclusions based on the saproxylic community colonizing deadwood at early decay stages. According to Hjältén et al. (2007) our results illustrate the importance of substrate characteristics to saproxylic beetle species richness at early successional stages but this does not necessarily reflect long-term responses of saproxylic beetles to forest management. Therefore, future research should be conducted on intermediate and late deadwood decay stages. With advancing decomposition tree specific characteristics of the deadwood items become less pronounced, thus saproxylic diversity of late decay stages might depend on other drivers as early successional beetles (Vanderwel *et al.* 2006). Proof for this suggestion is given by the investigations concerning the beetle *Osmoderma eremita*, which inhabits deadwood of late successional stages and specialised not on particular tree species, but on substrate conditions (Chiari *et al.* 2012). As the structure of later successional deadwood typically is defragmented and therefore prone to dry out, associated saproxylic beetles might prefer shaded stumps and logs instead of sun-exposed items. Furthermore, we investigated downed deadwood logs, but disregarded the saproxylic fauna inhabiting snags, stumps or deadwood within the canopy. As shown by several studies, different deadwood structures host distinct saproxylic beetle assemblages. Thus, to fully understand the impacts of forestry on saproxylics and their species-specific functions, other deadwood structures should also be taken into account.

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AUTHOR CONTRIBUTIONS

Chapter II

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Beate Wende, Martin M. Gossner, Iris Gallenberger, Andreas Floren, Karl Eduard Linsenmair, Wolfgang W. Weisser, and Ingolf Steffan-Dewenter. Saproxylic beetle diversity in temperate forests: effects of tree species identity, management and geographic region

The work distribution among authors was as follows

MG, AF, KEL & WW designed the experiment; BW set up the experiment; BW did the field work, BW performed the statistical analysis; BW wrote the manuscript; MG, IG, AF, KEL, WW & ISD proof-read the manuscript.

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Chapter III

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MG, AF, KEL & WW designed the experiment; BW set up the experiment; BW did the field work, BW performed the statistical analysis; BW wrote the manuscript; MG, AF, KEL, WW & ISD proof-read the manuscript.

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The work distribution among authors was as follows

MG, AF, KEL & WW designed the experiments; BW set up the experiments; BW did the field work, MG analyzed the GIS-data; BW, performed the statistical analysis; BW wrote the manuscript; MG, AF, KEL, WW & ISD proof-read the manuscript.

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2. In prep:

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3. In prep:

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   Effects of local and regional landscape structure on saproxylic beetle diversity.

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