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Biodiversity of dead-wood dependent insects – effects of forest management and prospects of conservation

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Zusammenfassung

Jahrhunderte menschlicher Nutzung haben Waldökosysteme weltweit sowohl bezüglich ihrer Ausdehnung als auch ihrer strukturellen Ausstattung verändert. Besonders Menge und Art des vorkommenden Totholzes unterliegt starkem menschlichem Einfluss. Diese anthropogenen Veränderungen zeigen deutliche Auswirkungen auf die Populationen vieler Waldarten und insbesondere totholzabhängiger (xylobionter) Arten. Totholzbewohner machen rund ein Viertel aller im Wald lebender Tierarten aus und sind von großer funktionaler Bedeutung für Ökosystemprozesse wie den Abbau von Holz und damit auch für Kohlenstoff- und Nährstoffkreisläufe. Um die Vielfalt xylobionter Arten zu erhalten, ist es notwendig, die Wirkungsbeziehungen und Zusammenhänge zwischen Umweltfaktoren, Artengemeinschaften und menschlichen Aktivitäten besser zu verstehen und darauf basierende Naturschutzstrategien zu entwickeln.

Im ersten Artikel, habe ich den Rote-Liste-Status xylobionter Käfer Deutschlands in Abhängigkeit von artspezifischen Eigenschaften, die Biologie und benötigte Ressourcen charakterisieren, unter Berücksichtigung der Phylogenie analysiert. Die Ergebnisse zeigten, dass das heutige Aussterberisiko von Totholzkäfern klar die ökologische Degradation der Wälder in Mittel- und Westeuropa im Zuge der modernen Forstwirtschaft der letzten Jahrhunderte widerspiegelt. Gefährdet sind große Arten, Arten des Tieflands und Arten mit kleinem Verbreitungsgebiet, sowie Arten, die besonntes, starkes oder Laubtotholz benötigen. Um xylobionte Käfer in Mittel- und Westeuropa zu schützen, sollte deshalb die Menge speziell dieser limitierenden Ressourcen erhöht, sowie Tieflagenwälder bevorzugt unter Schutz gestellt werden.

Der zweite Artikel stellt eine erste weltweite Literaturübersicht experimenteller Totholzforschung dar. Ziel dieses Artikels ist es, die bestehenden Erkenntnisse dieses Themenfeldes für Wissenschaftler und Praktiker zusammenzufassen und zukünftige Forschung durch das Aufzeigen von Wissenslücken zu lenken. Mittels einer Metaanalyse konnte gezeigt werden, dass sich aktive Totholzanreicherung positiv auf totholzabhängige Arten auswirkt, während weniger streng an Totholz gebundene Arten zwar im Mittel positiv, jedoch heterogener reagieren. Aus der Zusammenfassung der Literatur zeigt sich, dass Wissenslücken besonders in den Tropen, bezüglich später Holzzersetzungsphasen und artenreicher und funktional bedeutender Taxa wie Pilzen und Termiten bestehen. Anstatt weitere Experimente zu initiieren, könnten Ergebnisse bezüglich später Zersetzungsphasen

und zusätzlicher Artengruppen schneller und effizienter erzielt werden, wenn bereits etablierte Experimente genutzt würden.

Für den Schutz von Totholzbewohnern ist es wichtig zu verstehen, ob der positive Zusammenhang zwischen Artenvielfalt und Totholzmenge auf höhere Ressourcenverfügbarkeit (*species-energy hypothesis*) oder höhere Habitatheterogenität (*habitat-heterogeneity hypothesis*) zurückzuführen ist. Da Totholzmenge und Totholzvielfalt meist korreliert sind, wurde ein im dritten Artikel beschriebener experimenteller Ansatz verfolgt, für den Menge und Vielfalt von Totholz in sonnigen und schattigen Waldbeständen manipuliert wurde. Dabei zeigte sich, dass Habitatheterogenität der treibende Faktor der Artenvielfalt ist und dass der Grad der Besonnung die Zusammensetzung der xylobionten Käfergemeinschaften bestimmt. Positive Effekte der Habitatheterogenität zeigten sich sowohl durch direkte Erhöhung der Totholzvielfalt bezüglich Baumart und Durchmesser, als auch durch Erhöhung der Totholzmenge, da mit steigender Totholzmenge die Habitatheterogenität bezüglich Temperatur und Holzfeuchte erhöht wurde. Schutzkonzepte für xylobionte Käfer, sollten daher die Erhöhung der Habitatheterogenität, direkt oder indirekt über die Totholzmenge, sowie die Bereitstellung von Totholz entlang des gesamten Kronenschlussgradienten zum Ziel haben.

Da Totholz für die meisten xylobionten Arten nur für begrenzte Zeit die benötigten Eigenschaften aufweist, benötigen xylobionte Insekten eine hohe Fähigkeit, geeignete Substrate zu finden. Im vierten Artikel untersuchte ich die Lockwirkung von holzbesiedelnden Pilzen und verschiedenen Totholztypen auf Rindenwanzen. Obwohl sich diese von Pilzen ernähren, zeigte die Abundanz von Pilzfruchtkörpern, die auch der Häufigkeit von Pilzmyzel entsprach, keinen Einfluss auf die Häufigkeit der Wanzen. Stattdessen nahm die Abundanz der Wanzen mit steigender Oberfläche starken Totholzes zu und war zudem auf besonnten Flächen höher als auf schattigen. Dies ist ein Hinweis darauf, dass holzbewohnende Wanzen zu Beginn der Sukzession neue Ressourcen anhand holzbürtiger Merkmale, vermutlich Duftstoffe, finden. Es ist jedoch möglich, dass die gefundenen Substrate anschließend anhand weiterer Merkmale auf ihre Eignung untersucht werden.

Forstwirtschaft und Naturschutzmaßnahmen können die Zusammensetzung und Diversität totholzbewohnender Artengemeinschaften stark beeinflussen. Im fünften Artikel konnte gezeigt werden, dass sich Totholzkäfergemeinschaften in borealen Wäldern nach Kahlschlag, Nutzung mit Belassen von Überhältern und kontrolliertem Abbrennen bezüglich biologischer Arteigenschaften, Ressourcenpräferenzen und phylogenetischer

Zusammensetzung unterscheiden. Während Feuer und das Belassen von Überhältern spezialisierte Artengemeinschaften mit ähnlichen Präferenzen erzeugte, wurden Kahlschläge von dem Zufall entsprechenden Artengemeinschaften ohne klare Präferenzen besiedelt. Um Lebensraum für Artengemeinschaften früher Waldentwicklungsphasen bereitzustellen, sollten unterschiedliche Mengen an Überhältern bei der forstlichen Nutzungen belassen werden. Zudem sollte ein Teil der Bestände zusätzlich abgebrannt werden.

Die vorliegende Arbeit deckt eine weite Brandbreite verschiedener Wald-ökosysteme ab und gibt deutliche Einblicke, wie Umweltfaktoren und menschliche Aktivitäten die Diversität und Zusammensetzung von totholzbewohnenden Artengemeinschaften beeinflussen. Basierend auf diesen Ergebnissen, konnte eine Reihe von neuen Empfehlungen für Förster, Naturschützer und politische Entscheidungsträger entwickelt werden, die dazu beitragen können, Naturschutzkonzepte zur Erhaltung der Biodiversität von Totholzbewohnern zu verbessern.

Summary

Over centuries, human activities have changed the extent and characteristics of forests all over the globe. In forests today, the quantity and types of occurring dead wood is largely determined by human management. These anthropogenic changes have affected many forest species and especially saproxylic, i.e. dead-wood dependent, species. Saproxylic species comprise about one quarter of forest biodiversity and are functionally important for ecosystem processes such as wood decomposition, nutrient and carbon cycling. To maintain biodiversity and ecosystem functioning associated with dead wood by evidence-based and efficient conservation strategies, the relationship between environmental factors, species and human management has to be well understood.

In the first article, I linked the red list status of saproxylic beetles in Germany to biological and resource-related species' traits while accounting for phylogenetic relatedness. This analysis showed that the extinction risk of saproxylic beetles in Central and Western Europe closely mirrors the ecological degradation of forests caused by forest management over the last centuries. In particular, large-bodied and lowland species, species with a small range and species that require sun-exposed, large-diameter or broad-leaved dead wood are more threatened. Conservation strategies across all forest types should thus strive to increase these limiting resource types and set-aside of forests for conservation should focus on lowland forests.

The second article, a first global review of experimental studies addressing biodiversity patterns in dead wood, sought to summarize existing knowledge for practitioners and researchers and to guide future research by identifying gaps in knowledge. The results indicate that global conservation of dead-wood associated taxa would benefit most by prioritizing research in the tropics, and other neglected regions, focusing on advanced stages of wood decomposition and assessing a wider range of taxa. Instead of initiating new experiments, results regarding advanced decay stages and additional taxa could be obtained quickly and with low effort when existing experimental set-ups are used. A meta-analysis of the effect of dead-wood addition on biodiversity revealed a consistently positive response of saproxylic taxa and overall positive but more heterogeneous response patterns of non-saproxylic taxa.

An important question for conservation of saproxylic species is if the positive relationship between dead-wood amount and species richness is due to an increase of resource availability (*species-energy hypothesis*) or habitat heterogeneity (*habitat-*

heterogeneity hypothesis) with increasing dead-wood amount. By experimental manipulation of dead-wood amount and dead-wood diversity described in the third article, I disentangled these naturally correlated factors. Results indicated that habitat heterogeneity is the major driver of species richness of saproxylic beetles and that habitat heterogeneity can be increased either indirectly by increasing the amount of dead wood or directly by intentional provision of dead wood of different tree species or diameter classes. Furthermore, microclimate clearly differentiated the composition of saproxylic beetle assemblages and thus, conservation strategies should aim at providing dead wood along the full gradient of canopy openness.

Dead wood is an ephemeral resource which requires a high ability of saproxylic insects to locate suitable substrates. In the fourth article, I evaluated the attraction of saproxylic heteropterans to wood-decaying fungi and different types of dead wood during the early stage of wood decomposition. Although saproxylic heteropterans are mycetophagous, the abundance of fungal fruit bodies, which was similar to the abundance of fungal mycelia, had no effect on the abundance of heteropterans. Instead, the abundance of saproxylic heteropterans increased with the surface area of dead wood of large diameter and was higher in sunny than in shady forests. This suggests that during the early phase of colonization, saproxylic heteropterans use wood-borne cues, most likely volatile chemicals, to locate new resources on larger distances. However, it is possible that after landing different cues are used to evaluate the suitability of particular logs on short range.

Forest management regimes and conservation measures can strongly affect the diversity and composition of saproxylic communities. In the fifth article, I could show that saproxylic beetle assemblages in boreal forest stands subject to clear-cutting, retention forestry or prescribed burning differed when characterized by biological and resource-related species' traits and phylogenetic relatedness. Burned stands and stands with retention trees hosted specialized assemblages with similar resource-requirements, while clear-cuts assembled rather random assemblages without clear preferences. To provide habitat for saproxylic beetle communities of early-seral forests, retention forestry should be applied with various retention levels and some stands should be burned.

Covering a broad range of forest ecosystems, this thesis provides new insights into how environmental factors and human management shape the diversity and composition of saproxylic assemblages. Based on these results, a framework of recommendations for forest managers, conservationists and political decision makers could be derived which allows improving conservation strategies for saproxylic biodiversity.

1 Introduction

Compared to leaves and other plant material, the decomposition of dead wood is a slow process which can take from several years under tropical climate (Chambers *et al.* 2000) to several centuries in boreal forests near the timberline (Niemelä, Wallenius & Kotiranta 2002). Dead wood, thus, often accumulates greatly in forest ecosystems reaching locally values of up to 500 m³ ha⁻¹ in European Beech forests (Christensen *et al.* 2005) or up to 1400 m³ ha⁻¹ in the temperate rainforests of western North America (Harmon *et al.* 1986). Worldwide, dead wood accounts for 73 ± 6 Pg of carbon (Pan *et al.* 2011) representing up to 20% of total carbon stocks (Harmon *et al.* 1986; Ulyshen 2014 and references therein).

1.1 Dead-wood associated taxa – diversity and function

Dead wood is a crucial element for biodiversity in forest ecosystems as the high amount of nutrients, energy and habitat space formed by dead wood allowed a large number of species to evolve an association with dead wood including both saproxylic species, i.e., directly or indirectly dependent on dying or dead wood, and non-saproxylic species (Stokland, Siitonen & Jonsson 2012). Among saproxylic taxa, wood-decaying fungi and arthropods account for the majority of species (Speight 1989; Boddy, Frankland & West 2008; Stokland, Siitonen & Jonsson 2012). In addition, vertebrates such as cavity-nesting birds depend on dead or dying trees (McComb & Lindenmayer 1999). Other non-saproxylic species such as litter-dwelling arthropods or molluscs use dead wood for shelter or nesting or benefit from microclimatic conditions near dead wood (Ulyshen *et al.* 2011). Additionally, many epixylic lichens, bryophytes and tree seedlings grow on dead wood (Andersson & Hytteborn 1991; Szweczyk & Szwagrzyk 1996; Spribille *et al.* 2008). As neither the total number of species on Earth is known, nor information on life history of many known species is available, it is obvious that no global estimates of the number of saproxylic species exist. For northern Europe, however, cautious estimates consider 20 to 25% of all forest species saproxylic (Siitonen 2001) and evaluations of certain well-studied taxa indicate that a similar or even higher proportion of forest species is saproxylic in temperate Europe, such as e.g. forest-dwelling beetles of which 56% are saproxylic (Köhler 2000).

Beetles are one of three hyperdiverse insect orders associated with dead wood which represent about 40% of all arthropod species (Grove & Stork 2000; Stokland,

Siitonen & Jonsson 2012) and there are probably more than twice the number of saproxylic beetle species than terrestrial vertebrates (Parker 1982). Saproxylic beetles are one of the best studied taxa associated with dead wood (Grove 2002; Stokland, Siitonen & Jonsson 2012). Beginning with Aldrovandi's "De Animalis Insecta" in 1602, a large body of literature has accumulated, particularly in Europe, including information on taxonomy, life history, habitat preferences and distribution of beetle species (Freude, Harde & Lose 1964-83; Koch 1989-92; Köhler & Klausnitzer 1998; Böhme 2005). Saproxylic beetles comprise a wide range of different functional groups including phloem- and wood-feeders, fungivores, predators or detritivorous species (Köhler 2000) and are thus involved in different ecosystem processes related to dead wood, such as wood decomposition (Ulyshen 2014). Habitat preferences of saproxylic beetle species – and similarly of other saproxylic arthropod groups such as saproxylic Heteroptera – differentiate between dead wood of different tree species, decay stages, wood diameter classes, microclimatic conditions and other criteria of dead wood (Möller 2009; Ulyshen & Hanula 2009; Gossner *et al.* 2013). Due to their sensitivity regarding dead-wood quality and quantity, saproxylic beetles are considered indicators for forest degradation worldwide (Grove 2002). Today, many saproxylic beetle species are red-listed in Europe but also in many other regions of the world (Nieto & Alexander 2010; Schmidl & Büche 2015). In some rare cases, the processes of decline have been well documented as for instance for *Rhysodes sulcatus*. The species disappeared from Great Britain about 2000 years ago at times of heavy deforestation and forest exploitation and continued its retreat from the European continent over the last centuries (Speight 1989). It is now one of ten saproxylic beetle species listed in Annex II of the Fauna-Flora-Habitat directive of the European Union. Besides this program, numerous national and regional conservation programs target saproxylic species (see 1.3).

Many saproxylic insects are highly specialized to certain resource types or stages of wood decay (Möller 2009; Stokland, Siitonen & Jonsson 2012). For such species, the required type of dead wood represents an ephemeral habitat and its colonization requires a high tracking and dispersal ability (Ranius, Martikainen & Kouki 2011). Saproxylic insects use mostly olfactory and visual cues to find a suitable substrate (Bernays & Chapman 1994), but the efficiency in detecting suitable structures varies greatly between species and spatial scales (Saint-Germain, Buddle & Drapeau 2007). On larger spatial scales, volatile chemicals are primary attractants for many species, while on smaller spatial scales, most species land randomly to assess the quality of the potential host tree through gustatory or

short-range olfactory cues (Saint-Germain, Buddle & Drapeau 2007). The origin of the volatile chemicals used to locate the required type of resource depends on the species' habitat requirements. Thus, species living in fresh dead wood, such as bark beetles, use volatile chemicals emitted by weakened trees or fresh dead wood (Renwick & Vite 1969), while species of later successional stages, many of which are mycetophagous, are attracted to volatile chemicals emitted from decaying wood and/or associated fungi (Guevara, Rayner & Reynolds 2000; Leather *et al.* 2014). The ability to differentiate between different substrates by olfactory cues is highly developed in some species being able to differentiate between fruit bodies of different fungal species or between fruit bodies and mycelia of the same fungal species (Guevara *et al.* 2000; Jonsell, Schroeder & Weslien 2005; Johansson, Olsson & Hjältén 2006).

Saproxyllic species play an important role for the decomposition of wood – a key process in forest ecosystems with regard to nutrient cycling and carbon storage (Harmon *et al.* 1986). In most terrestrial ecosystems, fungi are the most important decomposers of wood (Boddy, Frankland & West 2008; Stokland, Siitonen & Jonsson 2012). However, at levels of wood moisture below 30%, fungal decomposition is mostly inhibited (Schmidt 2006). Thus, in dry climatic regions, the importance of invertebrates, particularly termites, is pronounced compared to fungi which dominate in humid environments (Stokland, Siitonen & Jonsson 2012). However, also in humid environments as in many temperate forests, saproxyllic insects contribute significantly to wood decomposition (Ulyshen, Wagner & Mulrooney 2014; Ulyshen 2014). Overall, about 10–20% of wood mass loss is commonly attributed to decomposition by saproxyllic insects (Ulyshen 2014). Mechanisms how saproxyllic insects affect wood decomposition involve enzymatic digestion, substrate alteration or interactions with other taxa such as vectoring of wood-decaying fungi (Persson, Ihrmark & Stenlid 2011; Strid *et al.* 2014; Ulyshen 2014). However, a global analysis that accounts for differences in climate and in the distribution of species is still missing (Ulyshen 2014). This hampers predictions concerning the role of saproxyllic taxa for this important process under current and future climate change with further alterations of precipitation (Solomon *et al.* 2007).

1.2 Natural and anthropogenic drivers of dead-wood dynamics

In natural forest ecosystems, dead wood is frequently created by complete or partial die-off of senescent and old trees (Lindenmayer, Laurance & Franklin 2012; Müller *et al.* 2014) or by natural disturbances such as wildfires, insect outbreaks or windstorms which can affect

single trees or complete stands (White & Pickett 1985). Such events determine largely the spatial and temporal dynamics of dead wood in both broadleaf- and conifer-dominated forests (Schelhaas, Nabuurs & Schuck 2003; Šamonil *et al.* 2009; Seidl *et al.* 2014). Both senescence and natural disturbances can result in high dead-wood volumes, a high diversity of substrate types regarding, e.g., tree diameter, sun exposure or tree species, and specific resource types, such as charred wood after fire, uprooted trees after windthrows or rot holes in overmature trees (e.g., Menzel, Schulz & Taeger 2003; Ranius, Niklasson & Berg 2009; Müller, Jarzabek-Müller & Bussler 2013). This variety of resource types is crucial as it represents a wide range of habitats for saproxylic species.

In Europe, forests have been affected by humans for >5000 years (Grove 2002). Due to widespread forest clearance, forest cover reached its smallest extent since the last glacial maximum by around AD 1750 (Whitehouse 2006) and the demands placed on remaining forest patches have dramatically reduced the amount and diversity of dead wood at a wide range of scales (Siitonen 2001; Grove 2002; Lindenmayer, Laurance & Franklin 2012). With the beginning of modern forest management in the late 18th century, indigenous broad-leaved tree species were replaced by fast-growing conifers, and moribund and old trees were extracted (Grove 2002). Furthermore, forest management aimed at prevention of natural disturbances and dead wood created by disturbances is removed during salvage logging operations (Lindenmayer *et al.* 2004). The growing stock in European forests increased after World War II by more than 300%, although the forest area increased only slightly by about 10% (Schelhaas, Nabuurs & Schuck 2003). As a consequence of increasing growing stock, disturbance prevention and salvage logging, formerly open forests developed into shady even-aged stands and sun-exposed dead wood has become rare (Larsson 2001).

In boreal forests where fire represents the naturally dominant stand-replacing dynamic, disturbance prevention has been particularly effective. Instead of natural stand-replacing dynamics, clear-cut harvesting has been proposed as a harvesting system that closely mimics natural dynamics (Mielikäinen & Hynynen 2003), despite obvious differences in biological legacies such as dead trees (e.g., Franklin *et al.* 2000; Swanson *et al.* 2011). Over the last decade, the competition for woody resources has increased strongly due to high energy prices which in turn led to increased harvest of dead trees and logging residues, even of small diameter (Lassauce, Lieutier & Bouget 2012). Therefore, even if forests still cover a considerable portion of our landscape, structures of these production forests, particularly dead-wood amount and diversity, differ considerably from those of

pristine forests (Gossner *et al.* 2013). This highlights the importance of the few forest remnants largely unaffected by forest management in Europe and in adjacent regions as for instance the 1.8 million ha of Hyrcanian beech forest in northern Iran that are characterized by numerous old-growth features and a high proportion of saproxylic species extinct in Central Europe (Müller *et al.* 2015b).

1.3 Conservation of biodiversity in dead wood

Over the past 20–30 years, hundreds of articles have been published that provided insights into habitat preferences of saproxylic organisms and interactions within communities, demonstrating the linkage between losses of dead wood and declines in biodiversity (Siitonen 2001; Grove 2002; Davies *et al.* 2007; Müller & Bütler 2010; Lassauce *et al.* 2011; Stokland, Siitonen & Jonsson 2012). Due to these large efforts, the importance of dead wood for biodiversity has been widely acknowledged and conservation strategies focusing on dead wood are pursued in a number of countries, mostly in boreal and temperate regions of Europe and North America (Hutto 2006; Davies *et al.* 2007; Similä & Junninen 2012; Halme *et al.* 2013). As refuges of species most sensitive to forest management, the protection of the few pristine forest remnants in Europe and adjacent regions is the top priority for conservation of forest biodiversity (Siitonen 2001; Müller *et al.* 2015b). For large protected areas and to a lower extent also other forests, a strategy of benign-neglect regarding natural disturbances has been proposed implicating that structural characteristics created by such events as, e.g., dying and dead trees are not removed by forest management (Müller *et al.* 2010). This strategy accounts for the importance of early-successional stages and dead-wood legacies for biodiversity (Swanson *et al.* 2011; Thorn *et al.* 2015; Winter *et al.* 2015). In boreal forests, prescribed burning is practiced as a conservation tool to provide habitat for pyrophilous species (Hyvärinen, Kouki & Martikainen 2009) and green-tree retention is considered to mitigate effects of timber harvesting (Gustafsson, Kouki & Sverdrup-Thygeson 2010; Lindenmayer *et al.* 2012). For temperate and boreal forests, the amount of dead wood has been identified as a crucial factor for species richness, functional diversity and community composition of saproxylic species (Müller & Bütler 2010; Gossner *et al.* 2013; Bässler *et al.* 2014). Most conservation strategies in managed forests thus aim at reaching critical thresholds which range from 20 to 30 m³ ha⁻¹ for boreal forests and from 30 to 50 m³ ha⁻¹ for temperate forests in Europe (Müller & Bütler 2010). Measures to maintain or increase dead-wood volumes include retaining old, senescent and dead trees or logging residuals (Davies *et al.*

2007; Lindenmayer, Laurance & Franklin 2012; Müller *et al.* 2014) and active measures to create or accelerate the development of dead wood (Jonsson, Kruys & Ranius 2005; Davies *et al.* 2007; Bauhus, Puettmann & Messier 2009; Ranius *et al.* 2014). Particularly in Fennoscandia, trees are frequently topped, girdled or felled during forest restoration campaigns or regular timber harvests to create standing or downed dead wood (Jonsell, Nittérus & Stighäll 2004; Komonen *et al.* 2014). In contrast to such measures which cause the rapid death of a tree, measures that start a slow senescence process are rarely applied despite the importance of tree hollows and other microhabitats that develop during such a process and host many rare saproxylic species (Ranius, Niklasson & Berg 2009; Müller *et al.* 2014; Larrieu *et al.* 2014).

Most forest and conservation managers, however, are restricted by economic constraints and thus, conservation strategies have to be balanced between economic and biodiversity requirements (Jonsson *et al.* 2006; Ranius *et al.* 2014). To allocate conservation funds effectively, the major drivers behind large-scale extinction processes must be identified. For species threatened by anthropogenic habitat changes, a promising approach is to link the red-list status of species – as an ordinal index of extinction risk – to specific traits that connect species to resources they rely on (Fritz, Bininda-Emonds & Purvis 2009; Cardillo & Meijaard 2012). This allows the identification of resources that drive the extinction risk of species and targeting the increase of these limiting resources in conservation strategies. The efficiency of such strategies can be further increased by considering potential interactions between different dead-wood factors. Temperature, for instance, interacts with dead-wood amount, as species richness of saproxylic beetles increases more strongly with increasing dead-wood amount in cool than in warm climate and the same amount of dead wood hosts more species in warm than in cool regions (Müller *et al.* 2015a). This indicates that dead-wood addition should be more pronounced in cool than in warm climates. Further improvement of existing strategies focusing on dead-wood volume could possibly be achieved by untangling the role of dead-wood amount from that of dead-wood diversity, i.e., diversity regarding wood diameter, tree species, sun exposure or decay stage (Siitonen *et al.* 2000). If dead-wood diversity had an independent effect on biodiversity, conservation strategies could aim at the lower boundary of recommended dead-wood amounts (Müller & Bütler 2010) but maintain a high species richness of saproxylic species by maximizing the diversity of woody substrates. However, under natural conditions, the amount of dead wood is regularly correlated with dead-wood diversity, and thus, field studies based on survey data that used correlative analysis could

not dissect the independent effects of the two variables on species richness (Müller & Bütler 2010). Here, experimental approaches are needed to resolve the correlation between dead-wood amount and dead-wood diversity by active manipulation (Davies *et al.* 2007).

1.4 Studying biodiversity in dead wood

To study biodiversity in dead wood, both field surveys and field experiments involving manipulation of dead wood are frequently applied. Research on this topic started mostly with field surveys more than 30 years ago. Since then, this type of approach has contributed significantly to our knowledge of life in dead wood and has provided the basis for many existing conservation strategies targeting saproxylic biodiversity (e.g. Siitonen 2001; Grove 2002; Boddy, Frankland & West 2008; Junninen & Komonen 2011; Stokland, Siitonen & Jonsson 2012; Halme *et al.* 2013). However, causality of observed relationships is often difficult to prove by such approaches because of many possible confounding factors, such as differences in dead-wood type, age or management history among the studied stands, or when factors are correlated such as dead-wood amount and dead-wood diversity. In these cases, only clear standardized conditions and well-designed manipulations can reveal causalities and distinguish between the effects of different factors on species assemblages and ecosystem processes (Davies *et al.* 2007; Stephens *et al.* 2015). Experimental approaches have been increasingly applied over the last 10–15 years and the insights gained from these efforts, alongside those from observational studies, continue to inform and refine evidence-based conservation strategies (Similä & Junninen 2012; Halme *et al.* 2013). Manipulating high volumes of dead wood and maintaining standardized conditions over the full span of the decomposition process is often cost intensive and laborious. In particular, sufficiently replicated manipulations of dead wood may not always be realizable at large spatial and temporal scales (e.g., Gossner *et al.*, 2013b; Nordén *et al.*, 2013) and thus, field survey approaches are often without alternative (Stephens *et al.* 2015).

When experimental approaches are used to evaluate hypotheses based on general ecological theories, the obtained results can often be generalized broadly and can help to understand mechanisms behind observed ecological pattern (Stephens *et al.* 2015). For example the positive correlation of dead-wood volume and species richness of saproxylic species, as observed in many field surveys, can be explained either by the *more-individuals hypothesis* – a form of the *species-energy hypothesis*, or by the *habitat-heterogeneity hypothesis*. According to the former, the population sizes of species – and with it the

number of species – in a certain area increases with increasing availability of chemical energy, which is represented by the amount of resources available to each specific species (Wright 1983; Srivastava & Lawton 1998; Schuler, Chase & Knight 2015). Alternatively, the habitat-heterogeneity hypothesis predicts that the number of species increases with increasing habitat heterogeneity as an elevated number of niches allows for more species to coexist (e.g., Simpson 1949; MacArthur & MacArthur 1961; Tews *et al.* 2004). The correlation of resource availability and habitat heterogeneity is not only observed for dead wood, but is a general pattern (Wright 1983; Whittaker 1998) and thus, studies untangling the role of both mechanisms for saproxylic biodiversity may add to our general knowledge of species-environment relationships. Such understanding of ecological mechanisms driving species' responses to management or environmental changes can help to evaluate and improve management or conservation strategies to maintain biodiversity and ecosystem functioning (e.g., Bässler *et al.*, 2014).

2 Objectives

The basic aim of this thesis was to improve the understanding of basic ecological relationships between different facets of diversity and community structure of saproxylic insects and their environment. In particular, I focused on the role of forest management for saproxylic insects and/or habitat structures which are important for conservation of these taxa, such as dead-wood amount and dead-wood diversity. In this context, I also evaluated the effectiveness of specific management activities, such as dead-wood enrichment or prescribed burning, to provide habitat for saproxylic insect assemblages. Based on these results, I derived recommendations how strategies aiming at the conservation of saproxylic insect diversity can be improved. These recommendations target particularly production forests, but can also be applied in protected areas or to design financial incentives for conservation activities in private forests. The spatial focus ranged from a worldwide perspective via a review and meta-analysis of published data, to the level of certain biomes – namely temperate and boreal European forests – to montane mixed forests in Central Europe.

The specific objectives of this thesis were:

- i. To identify the main drivers behind large-scale extinction processes of saproxylic beetles in Central and Western Europe and to derive recommendations how practical conservation on a national level can be improved.
- ii. To identify global gaps in knowledge regarding experimental research on dead-wood biodiversity to guide future research and to summarize existing knowledge, particularly on dead-wood addition, for conservation practitioners and scientists.
- iii. To disentangle the effect of resource availability (dead-wood amount) and habitat heterogeneity (dead-wood diversity) on species richness of saproxylic beetles relative to microclimate to increase the efficiency of dead-wood accumulation strategies in managed forests.
- iv. To analyze habitat preferences of saproxylic heteropterans, a group with a high proportion of threatened species, and mechanisms how saproxylic insects locate and colonize ephemeral resources.

- v. To compare the effects of clear-cutting, prescribed burning and green-tree retention on the functional composition of saproxylic beetle communities in boreal forests to evaluate the efficiency of the two later strategies as conservation-oriented alternative to clear-cut harvesting.

3 Methods and study system

To achieve the objectives of this thesis, information on ecological traits, red-list status and phylogeny of European saproxylic beetle species was compiled from an existing database (Gossner *et al.* 2013) and from the literature. Furthermore, an extensive literature search was performed to detect all experimental studies focusing on biodiversity pattern in dead wood. From this body of literature, data was compiled on the effects of dead-wood addition on species richness of saproxylic and non-saproxylic taxa and analyzed pursuing a meta-analysis approach. To disentangle the effects of dead-wood amount and dead-wood diversity relative to microclimate on saproxylic insects, dead wood was exposed in a field experiment in the Bavarian Forest National Park and saproxylic beetles and heteropterans were sampled during the first three years after exposure of the dead wood. Finally, I applied a functional-phylogenetic approach to analyze data on saproxylic beetle communities from the FIRE experiment conducted in eastern Finland which comprised clear-cutting, prescribed burning and harvesting with green-tree retention as treatments.

3.1 Traits of saproxylic beetles in Europe

3.1.1 Red-list status

The German Red List of Beetles (Schmidl & Büche 2015) covers all saproxylic beetle families besides three saproxylic species of the families Carabidae and Rhysodidae for which an additional red list exists (Schmidt, J., Trautner, J. & Müller-Motzfeld, G. unpublished data). The categories of the German red list follow the International Union for Conservation of Nature (IUCN) classification and include the categories rare (R) and indeterminate (I), which were used by the IUCN until 2001. Of the 1405 saproxylic beetle species in Germany, 1064 species were assigned to a red-list category and 28% of them are listed as threatened or regionally extinct. Each of the categories contains the following number of species: regionally extinct (RE), 39 (4%); critically endangered (CR), 57 (5%); endangered (EN), 75 (7%); vulnerable (VU), 128 (12%); near threatened (NT), 63 (6%); and least concern (LC), 704 (66%). For further analyses of extinction risk, these categories were converted into an ordinal scale of extinction risk ranging from 0 (LC) to 5 (RE).

3.1.2 Species traits

Data on traits of saproxylic beetle species of central and northern Europe were compiled by extending the existing data base published by Gossner *et al.* (2013) to include additional

species and traits. The achieved data comprised eight biological and resource-related traits as well as geographic and elevational distribution in Germany (Table 1).

Table 1: List of species traits of saproxylic beetles with unit, range and the sources of the data.

Variable	Unit	Range or definition	Source
Range size	Numerical	0–18	Köhler (2011)
Elevation	Numerical	1–4	Böhme (2005)
Body size	mm	0.7–50.0	Gossner et al. (2013) completed after Freude et al. (1964-83)
Wood diameter niche	Numerical	1–4 (small–high)	Gossner et al. (2013) completed after Möller (2009)
Canopy niche	Numerical	1–3 (sunny–shady)	Gossner et al. (2013) completed after Möller (2009)
Decay niche	Numerical	1–5 (fresh–decomposed)	Gossner et al. (2013) completed after Möller (2009)
Flower visitor	Binomial	yes/no	Köhler (2000)
Host tree	Category	conifer, broad-leaved, both	Schmidl & Bußler (2004), completed after Köhler (2000)
Guild	Category	wood and bark, cavity, fungi	Schmidl & Bußler (2004) simplified, completed after Köhler (2000)
Feeding strategy	Category	xylophagous, mycetophagous, detritivorous, predatory	Köhler (2000) simplified

Traits which described required resources were mean niche positions with regard to wood diameter, decay stage of dead wood and canopy cover of forests in which a species occurs; preference of adult beetles to visit flowers; host-tree preference of species (coniferous, broad-leaved, or both types); and microhabitat guild of larvae (wood and bark, cavities, fungi). Biological traits comprised the mean body size and feeding strategy of larvae (xylophagous, mycetophagous, detritivorous, predatory). Furthermore, the number of German regions (maximum 18) in which a species was reported during the last 200 years was used as measure of range size and the mean elevational distribution was calculated from an ordinal scale of elevational zones (planar, colline, montane, and subalpine). The mean niche positions were calculated following the procedure of Gossner et al. (2013) by assigning the classes of each trait (diameter, <15, 15–35, 35–70, >70 cm; decay, alive, freshly dead, initiated, advanced decomposition, extremely decomposed; canopy cover, open, semi-open, closed) to an ordinal scale. For each species, each class was multiplied with a weighting score representing the frequency of occurrence in this particular class (0.5, very rarely used; 1, rarely used; 2, commonly used; 3, preferred) and divided by the

sum of the weighting scores. As an example, the calculation of the mean canopy niche position of the longhorn beetle *Rosalia alpina* is as follows:

Canopy cover:	open	semi-open	closed
Canopy class:	1	2	3
Weighting score:	3	2	0
Calculation of mean:	$(3 \times 1 + 2 \times 2 + 0 \times 3) / 5$		
Mean canopy niche:	1.4		

3.1.3 Phylogeny

Following the approach of Gossner et al. (2013), I created a topology based mainly on the comprehensive genetic phylogeny provided by Hunt et al. (2007) which comprises nearly 1,900 species, representing more than 80% of the world's recognized beetle families. This topology was extended using higher-resolution topologies of several subgroups [for Ciidae Buder et al. (2008); for Scolytinae Bussler et al. (2011); for Curculionidae Jordal et al. (2011); for Elateridae Kundrata & Bocak (2011), for Staphylinidae Chatzimanolis et al. (2010)], and by using additional information from a phylogeny based on morphology (Lawrence et al. 2011) and from taxonomic classification following the Catalogue of the Palearctic Coleoptera (Löbl & Smetana 2003-11) and Freude et al. (1964-83). Additional species were assigned to the tip next to the closest known relative. Because DNA sequence data were available only for a small subset of species, estimated branch lengths for the final topology were calibrated using 25 calibration points from fossil records using the function *bladj* in *phylocom* (Webb et al. 2008).

3.2 Literature review and meta-analysis

Considering standards for systematic reviews (Pullin & Stewart 2006), information on experimental dead-wood studies was compiled in April and updated in November 2014 by using the search string “forest AND (woody\$material OR woody\$biomass OR high\$stump OR snag OR woody\$debris OR dead\$wood OR CWD OR FWD) AND (accumulat* OR experiment* OR manipula* OR creat* OR artificial OR girdl*)”. By searching the databases ISI Web of Knowledge, JSTOR, Science Direct, Directory of Open-Access Journals, CAB Abstracts, Scopus and GeoRef, 1,267 publications were identified. From these, all relevant articles were identified by title (257), then by abstract (97) and finally by reading the full text. The obtained list was extended by examining references of these

articles for additional publications and by consulting experts from the global dead-wood ecology community to include running experiments that were not yet published. I only included studies which evaluated biodiversity patterns in terrestrial ecosystems, either of abundance, species number, species composition or functional composition, by conducting a field experiment. A study was considered experimental when either the amount or diversity of dead wood was manipulated by exposure or creation in situ, either explicitly by researchers or during regular management activities, as long as pre-treatment conditions and manipulations resulted in highly standardized conditions.

For each study that manipulated the amount of dead wood, I compiled mean species richness and standard deviation of various saproxylic and non-saproxylic taxa for the untreated control and the plots with the maximum level of added dead wood, as well as information on the number of plots and time since addition of dead wood. Data were extracted directly from published text or tables or from graphs using PLOT DIGITIZER 2.6.2 (www.plotdigitizer.sourceforge.net); authors were contacted to provide data if necessary. Multiple entries per experiment were possible when the experiment evaluated different conditions, such as open and closed forest; when multiple taxonomical groups were studied; or when the effect of the treatment was studied for more than one year. For handling of nested designs see section 3.5.

3.3 Bavarian Forest Dead-wood Experiment

3.3.1 Study area and experimental design

In autumn 2011, 190 0.1 ha plots were established within five blocks in a block random design across the Bavarian Forest National Park in south-eastern Germany (Fig. 1). Blocks were located within the zone of montane mixed forest dominated by European Beech (*Fagus sylvatica* L.), Silver Fir (*Abies alba* Mill.) and Norway Spruce (*Picea abies* (L.) H.Karst) between 715 and 1200 m a.s.l. (Seibold *et al.* 2013). Total annual precipitation ranges between 1300 and 1700 mm and mean annual temperature varies between 3.8 and 5.8°C (Bässler *et al.* 2009). To account for effects of microclimate (Vodka, Konvicka & Cizek 2008; Müller *et al.* 2015a), half of the plots within each block (i.e., 19) were established in a sunny clearing, and the other half were established in a mature beech forest under a closed canopy (Fig. 1). Dead wood was added to each plot which was freshly cut less than eight weeks before deposition and included logs (diameter: 25–50 cm, length: 5 m) of beech and/or fir and/or branches (diameter: 3–5 cm, length: 2–3 m) of one or both

tree species. Besides a control plot in which no wood was added, each plot contained either a low or high amount of branches (8 branches, about $0.2 \text{ m}^3 \text{ ha}^{-1}$ or 80 branches, about $2 \text{ m}^3 \text{ ha}^{-1}$) or logs (4 logs, about $10 \text{ m}^3 \text{ ha}^{-1}$ or 40 logs, about $100 \text{ m}^3 \text{ ha}^{-1}$) or a combination of logs and branches of low or high amounts (Fig. 1).

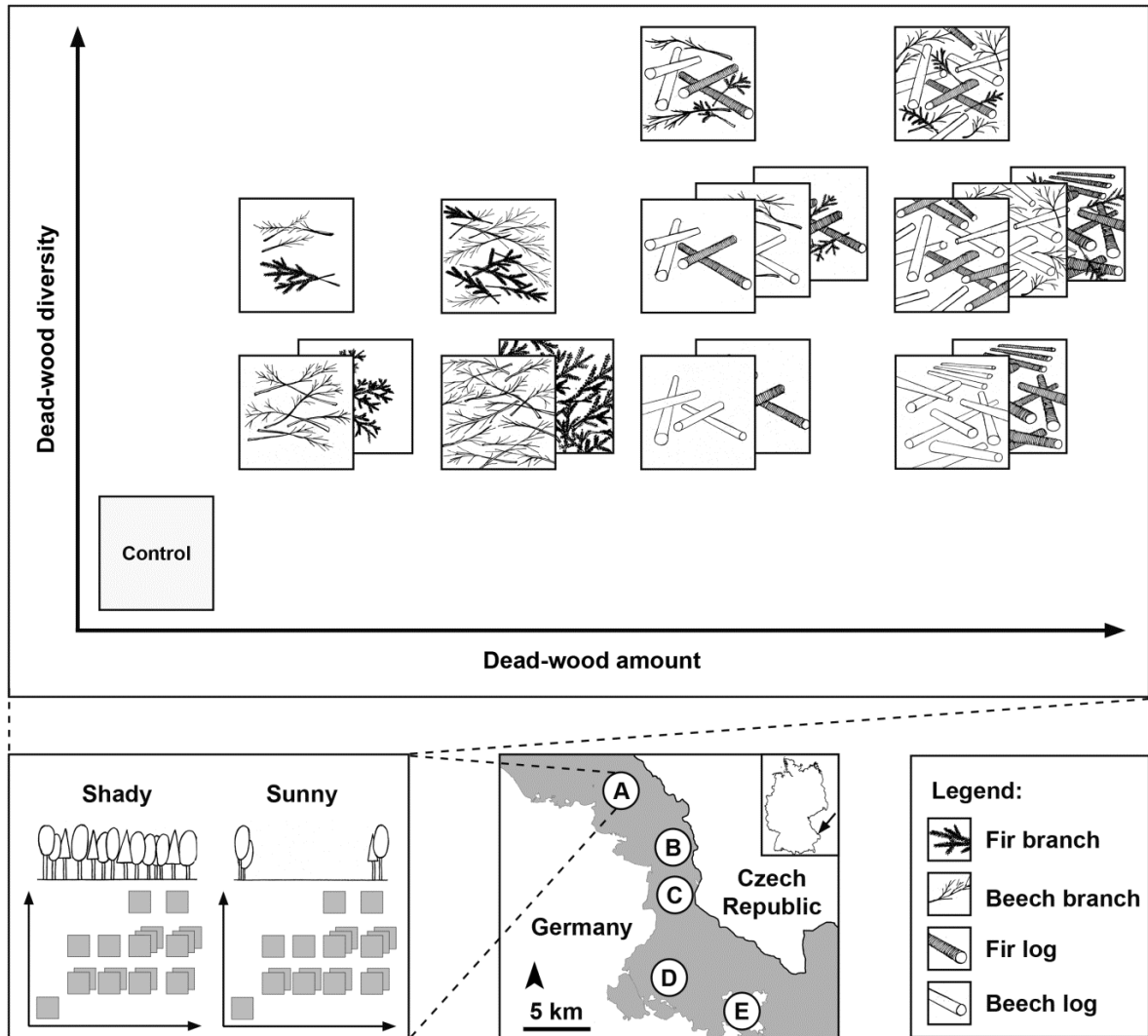


Figure 1: Location and design of the Bavarian Forest Dead-wood Experiment comprising nineteen combinations of dead-wood amount and dead-wood diversity in both sunny and shady forest plots (bottom left) replicated five times in a block random design (A–E; bottom centre). Dead-wood diversity was characterized as number of different substrate types, i.e., tree species (European beech or silver fir) and diameter classes (branch or log), per plot following Siitonen et al. (2000). Dead-wood amount is the total surface area of dead wood per plot. In the inset in the map, the black arrow indicates the location of the Bavarian Forest National Park in Germany.

Moreover, combinations of the four substrate types were realized to form a gradient of dead-wood diversity comprising three different levels. The lowest level of dead-wood diversity comprised only one of each of the four substrate types (beech logs, beech branches, fir logs, fir branches) and the intermediate level comprised either both diameter classes of the same tree species (beech logs and branches, fir logs and branches) or only one diameter class of both tree species (beech and fir logs, beech and fir branches; Fig. 1). The highest level of diversity comprised logs and branches of both tree species. Half of logs were placed on top of others such that some had full soil contact, whereas others were partly elevated and therefore comparatively dry (Möller 2009). Each sunny plot was mowed once a year during the growing season to avoid strong shading by a dense grass layer. To characterize precisely the amount of dead wood per plot, diameter and length of all logs and of a subsample of branches were measured to calculate the surface area of dead wood per plot (Heilmann-Clausen & Christensen 2004).

3.3.2 Sampling of saproxylic insects

Flying and flightless insects were sampled by two flight-interception traps and two pitfall traps on each plot. Two flight interception traps have proved to yield a sufficient number of specimen to obtain good correlations of diversity measures with local habitat conditions (Müller & Brandl 2009), particularly when complemented with pitfall traps for flightless species (Buse 2012). Traps were arranged in two groups 5 m apart at the centre of each plot, and each group consisted of one trap of each type. Each flight-interception trap consisted of a crossed pair of transparent plastic shields (40 cm × 60 cm) and was hung freely from ropes or poles about 50 cm above ground near the dead wood. Pitfall traps consisted of a 400 ml PP cup sunk flush with ground level with a PVC roof placed over it about 5 cm above ground level to shield from rain. Flight-interception traps were functional for the complete growing season and were emptied once a month. Pitfall traps were operated during May, July, and September. In both trap types, a non-attracting 3% copper sulfate solution was used to kill and preserve trapped insects. Sampling was conducted during the first three years of succession starting in 2012, i.e. the first spring after the dead wood was added. Catches were sorted into taxonomic groups at the order level and identified to species level by experts. Beetles (283,243 individuals, 1,722 species) were identified by Boris Büche and Dr. Alexander Szallies over the complete study time and saproxylic heteropterans (223 individuals, 6 species) were identified by Dr. Martin M. Gossner during the first two study years. Beetle data was divided into saproxylic

species according to reference lists (Köhler 2000; Schmidl & Bußler 2004) and phytophagous species of the families Elateridae, Chrysomelidae, and Curculionidae, which strictly feed on green plant tissue or living roots, as a control group.

3.4 Fire and green-tree retention in boreal forests – the FIRE experiment

The FIRE experiment was conducted in the middle-boreal zone of Eastern Finland (e.g., Hyvärinen *et al.* 2005; Hyvärinen, Kouki & Martikainen 2006). On an area of 20 km x 30 km, 24 Scots pine (*Pinus sylvestris* L.) dominated forest stands, each 3-5 ha, which had not been subject to intensive forestry before were selected for the experiment. Following the before-after-control-impact (BACI) principle (Green 1979), two treatments were applied: prescribed burning and four levels of harvesting (clear-cutting, 10 and 50 m³ ha⁻¹ retention, and unharvested control). Harvesting was conducted in winter 2000/2001 and each harvesting level was replicated six times. Half of the stands were subsequently burned in late June 2001 (Hyvärinen *et al.* 2005). The amount of retention trees was chosen as to be either comparable with current guidelines and industry-certification regulations in Fennoscandia (10 m³ ha⁻¹) or to reach thresholds of dead-wood volume identified to maintain the diversity of saproxylic beetles in boreal forests (50 m³ ha⁻¹; Martikainen *et al.* 2000; Müller & Bütler 2010). Saproxylic beetles were sampled in the years 2000 and 2002, i.e., one year before and one year after the treatments, using ten flight-interception traps per stand. Traps were operated from mid-May to early September each year and all trapped individuals were identified to the species level (Hyvärinen *et al.* 2005; Hyvärinen, Kouki & Martikainen 2006).

3.5 Statistical analyses

To achieve the objectives of this thesis, different statistical methods were applied and most analyses were conducted in R (Development Core Team 2014). For the analysis of the extinction risk of saproxylic beetles in Central and Western Europe (Article 1), a proportional-odds linear mixed effects model was applied. Linear mixed models were used to model Hedges' d standardized effect sizes for the meta-analysis of the effects of dead-wood addition on biodiversity (Article 2). To model the effects of dead-wood factors and microclimate on saproxylic insects, generalized linear mixed poisson models were calculated for count data and linear mixed models for normally distributed data of the

Bavarian Forest Dead-wood Experiment (Article 3 and 4). Linear models were also fitted for normally distributed community means of traits and standardized effect sizes of functional and phylogenetic diversity of saproxylic beetles relative to treatments of the FIRE-experiment (Article 5).

3.5.1 Proportional-odds linear mixed-effects model

Analysis of red-list categories – as an ordinal index of extinction risk (Verde Arregoitia, Blomberg & Fisher 2013) – are faced with two methodological problems. First, for modeling an ordinal response variable with probably unequal differences between consecutive levels (Matthews *et al.* 2011), ordinal regression models (Verde Arregoitia, Blomberg & Fisher 2013) or transformation of the response variable are needed (Mooers, Faith & Maddison 2008). Second, cross-species analyses have to account for phylogenetic relatedness as related species are statistically not independent (Freckleton *et al.* 2002). To model the extinction risk of 1025 saproxylic beetle species relative to all ten species traits described in Table 1, a proportional-odds linear mixed effects model was applied (Tutz 2011). The model accounted for the phylogenetic relatedness of species by including species-specific intercepts with a fixed correlation structure defined by the phylogenetic distance between each pair of species (Harvey & Pagel 1991; Fahrmeir, Kneib & Lang 2004). This modeling framework allowed estimation of extinction risk for 188 species without red-list status based on their traits and the phylogeny.

3.5.2 Hedges' d standardized effect size

To evaluate the effect of dead-wood addition on species richness relative to the control, I calculated Hedges' d standardized effect size based on the mean and standard deviation of species richness and the number of plots (Hedges & Olkin 1985). Hedges' d is a frequently applied measure in meta-analyses as it accounts for differences in sampling effort across studies and for small sample sizes (Hedges, Gurevitch & Curtis 1999). Positive values of Hedges' d indicate higher species richness on plots with added dead wood, whereas negative values indicate lower species richness. A mean effect size of $d = 0.2$ indicates a small effect, $d = 0.5$ indicates a moderate effect and $d = 0.8$ indicates a large effect (Koricheva *et al.* 2013).

3.5.3 Linear models

Depending on the type and structure of data, I applied different types of linear models in the different articles. For the meta-analysis, Hedges' d effect sizes were modelled by using a linear mixed-effects model with time since addition of dead wood and association of taxa with dead wood (saproxylic or non-saproxylic) as moderators to test whether the response of saproxylic and non-saproxylic taxa differed. To control for repeated measurements within one larger experiment, e.g., when various species groups were recorded, experiment was included as a random effect in the model (Viechtbauer 2010).

To evaluate the effects of the different dead-wood addition treatments and microclimate on abundance and species richness of saproxylic insects of the Bavarian Forest Dead-wood Experiment, I applied generalized linear mixed models with a Poisson error distribution with plot nested in block as random effects and a observation-specific random effect to account for the nested design (Fig. 1) and repeated measurements in consecutive years and for possible overdispersion (Elston *et al.* 2001). Models of species richness used the number of species as response variable and included the log-transformed abundance as predictor. By applying a similar linear mixed model, I evaluated treatment effects on the structure of saproxylic beetle assemblages which was characterized by the first axis of an ordination obtained by non-metric multidimensional scaling (NMDS; Oksanen *et al.* 2009) of presence-absence data.

Changes in the functional composition (see 3.5.4) of saproxylic beetle assemblages due to treatments of the FIRE-Experiment were assessed by linear models as both standardized effect sizes of functional-phylogenetic diversity and community-means of single traits were normally distributed. In these models, I set the data of the pre-treatment year 2000 as a baseline to compare treatment effects and to account for initial differences between study stands.

3.5.4 Phylogenetic and functional diversity

To characterize the functional composition of saproxylic beetle assemblages of the FIRE-Experiment while accounting for potential differences between assemblages contributed to unmeasured traits, we applied a recently proposed approach to combine functional and phylogenetic information (Cadotte, Albert & Walker 2013). Functional and phylogenetic distance matrices were calculated as mean pairwise distances between co-occurring species for each stand and year, based on either the branch lengths of a phylogenetic tree or a Gower distance – suitable for numerical and categorical variables – of two biological traits

and four traits describing required resources. The contribution of the single matrices to the combined mean functional-phylogenetic distance (MFPD) is defined by the weighting parameter a (when $a = 0$ only functional, and when $a = 1$ only phylogenetic distances are included). MFPD was calculated for 41 levels of a from 0 to 1 by increasing a in steps of 0.025.

To gain independence from species numbers, I calculated standardised effect sizes of MFPD (Laliberté & Legendre 2010; Mouillot *et al.* 2012) by applying a null model approach. It compares observed values of MFPD with those of randomly selected species assemblages of equal species number from the regional species pool (all species recorded in the data) using null models with 999 randomisations by tip shuffling (Kembel *et al.* 2010). Obtained effect-size values of functional-phylogenetic diversity >0 indicate over-dispersion, whereas values <0 indicate clustering (Pausas & Verdú 2010). Furthermore, to evaluate community shifts regarding single traits relative to the treatments, I calculated the abundance-weighted mean and the standardized effect size of diversity of each of the four numerical traits (i.e. excluding the two categorically measured traits) for each assemblage.

4 Manuscript overview

This thesis contains five published or accepted articles. For each article, a brief summary, the publication status and the contribution of the authors is provided in this chapter. A number of six additional articles within a larger framework of dead-wood ecology and two papers on general topics of ecology and conservation were published during the time span of this thesis and are listed in Appendix I.

Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe

Sebastian Seibold, Roland Brandl, Jörn Buse, Torsten Hothorn, Jürgen Schmidl, Simon Thorn and Jörg Müller

Published 2015 in Conservation Biology 29, 382-390. doi: 10.1111/cobi.12427.

Impact factor 2014: 4.165 (Rank 5 in Biodiversity Conservation)

To reduce future loss of biodiversity and to allocate conservation funds effectively, the major drivers behind large-scale extinction processes must be identified. A promising approach is to link the red-list status of species and specific traits that connect species of functionally important taxa or guilds to resources they rely on. Such traits can be used to detect the influence of anthropogenic ecosystem changes and conservation efforts on species, which allows for practical recommendations for conservation. We modeled the German Red List categories as an ordinal index of extinction risk of 1025 saproxylic beetles with a proportional-odds linear mixed-effects model for ordered categorical responses. In this model, we estimated fixed effects for intrinsic traits characterizing species biology, required resources, and distribution with phylogenetically correlated random intercepts. The model also allowed predictions of extinction risk for species with no red-list category. Our model revealed a higher extinction risk for lowland and large species as well as for species that rely on wood of large diameter, broad-leaved trees, or open canopy. These results mirror well the ecological degradation of European forests over the last centuries caused by modern forestry, that is the conversion of natural broad-leaved forests to dense conifer-dominated forests and the loss of old growth and dead wood. Therefore, conservation activities aimed at saproxylic beetles in all types of forests in Central and Western Europe should focus on lowlands, and habitat management of forest stands should aim at increasing the amount of dead wood of large diameter, dead wood of broad-leaved trees, and dead wood in sunny areas.

SS and JM developed the idea, SS collected data on traits and phylogeny. SS and TH developed the R code and wrote the respective section. SS, RB and JM performed the analyses and SS wrote the manuscript. JM, RB, ST, JS and JB contributed to improving later drafts.

Experimental studies of dead-wood biodiversity – a review identifying global gaps in knowledge

Sebastian Seibold, Claus Bässler, Roland Brandl, Martin M. Gossner, Simon Thorn,
Michael D. Ulyshen and Jörg Müller

Published 2015 in Biological Conservation 191, 139-149. doi: 10.1016/j.biocon.2015.06.006.

Impact factor 2014: 3.762 (Rank 6 in Biodiversity Conservation)

The importance of dead wood for biodiversity is widely recognized but strategies for conservation exist only in some regions worldwide. Most strategies combine knowledge from observational and experimental studies but remain preliminary as many facets of the complex relationships are unstudied. In this first global review of 79 experimental studies addressing biodiversity patterns in dead wood, we identify major knowledge gaps and aim to foster collaboration among researchers by providing a map of previous and ongoing experiments. We show that research has focused primarily on temperate and boreal forests, where results have helped in developing evidence-based conservation strategies, whereas comparatively few such efforts have been made in subtropical or tropical zones. Most studies have been limited to early stages of wood decomposition and many diverse and functionally important saproxylic taxa, e.g., fungi, flies and termites, remain under-represented. Our meta-analysis confirms the benefits of dead-wood addition for biodiversity, particularly for saproxylic taxa, but shows that responses of non-saproxylic taxa are heterogeneous. Our analysis indicates that global conservation of organisms associated with dead wood would benefit most by prioritizing research in the tropics and other neglected regions, focusing on advanced stages of wood decomposition and assessing a wider range of taxa. By using existing experimental set-ups to study advanced decay stages and additional taxa, results could be obtained more quickly and with less effort compared to initiating new experiments.

SS developed the idea and performed the literature search, the meta-analysis and wrote the first draft of the manuscript. All other authors contributed significantly to improve later drafts.

Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood

Sebastian Seibold, Claus Bässler, Roland Brandl, Boris Büche, Alexander Szallies, Simon Thorn, Michael D. Ulyshen, Jörg Müller

Accepted for publication at Journal of Applied Ecology.

Impact factor 2014: 4.564 (Rank 20 in Ecology)

Resource availability and habitat heterogeneity are principle drivers of biodiversity but their individual roles often remain unclear since both factors are usually correlated. The biodiversity of species dependent on dead wood could be driven by either resource availability represented by dead-wood amount or habitat heterogeneity characterized by dead-wood diversity or both. Understanding their roles is crucial for improving evidence-based conservation strategies for saproxylic species in managed forests. To disentangle the effects of dead-wood amount and dead-wood diversity on biodiversity relative to canopy openness (microclimate), we experimentally exposed different amounts of logs and branches of two different tree species representing a gradient of dead-wood diversity in 190 sunny and shady forests plots. During the three years after exposing dead wood, we sampled saproxylic beetles, which are together with fungi the most diverse and important taxonomic group involved in decomposition of wood. The composition of saproxylic beetle assemblages differed clearly between sunny and shady forest plots, with higher richness in sunny plots. Both dead-wood amount and dead-wood diversity positively and independently affected species richness of saproxylic beetles, but these effects were mediated by canopy openness. In sunny forest, species richness increased with increasing amount of dead wood, whereas in shady forest, dead-wood diversity was the prevailing factor. The step-wise analysis of abundance and species richness, however, indicated that effects of both factors supported only the habitat-heterogeneity hypothesis, as the positive effect of high amounts of dead wood could be explained by cryptic variability of dead-wood quality within single objects. As canopy openness and habitat heterogeneity seem to be the major drivers of the diversity of saproxylic beetles in temperate forests, we recommend that managers should aim to increase the heterogeneity of dead-wood substrates under both sunny and shady forest conditions. Intentional opening of the canopy should be considered in anthropogenically homogenized, dense forests. Specifically in

temperate mixed montane forests, dead wood should be provided in the form of large logs in sunny habitats and a high diversity of different dead-wood substrates should be retained or created in shady forests.

SS, JM, CB and RB developed the experimental design and installed the experiment. SS conducted field work. AS and BB identified sampled beetles. SS analyzed the data and wrote the manuscript. JM, CB, RB, AS, BB, ST and MDU contributed to improve the manuscript.

Wood resource and not fungi attract early-successional saproxylic species of Heteroptera – an experimental approach

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The availability of dead wood and ability to colonize these ephemeral structures are crucial for sustaining vital populations of saproxylic insects. These insects locate suitable resources mostly visually and via olfactory cues emitted by dead wood and/or wood-decaying fungi. For the conservation of saproxylic species of Heteroptera, a poorly studied group with a high proportion of threatened species, it is crucial to know which dead-wood structures are needed and how they are detected and colonized. In a field experiment, we exposed different amounts of dead-wood logs and branches of the main tree species of montane beech forests (*Abies alba*, *Fagus sylvatica*) on sunny and shady forest plots. We sampled saproxylic heteropterans and sporocarps of wood-decaying fungi in two consecutive years to test the hypothesis that early-successional saproxylic heteropterans are more attracted to wood-decaying fungi than to wood itself. The activity densities of saproxylic heteropterans measured with flight- interception traps increased with increasing surface of coarse woody debris and was higher under sunny conditions. Tree species, fine woody debris and abundance of sporocarps had no significant effect. Our results suggest that during the early-successional forest stage, dead wood provides more important cues than fungi in the search of saproxylic heteropterans for suitable hosts despite assumed close associations of the insects and certain fungal species. To improve habitats for saproxylic heteropterans, we recommend increasing the supply of dead wood of large diameter (>30 cm) in montane beech forests, particularly in sunny gaps. This can easily be realized during logging operations by gap felling.

SS, JM, CB and RB developed the experimental design and installed the experiment. SS collected data on heteropterans in the field and MMG identified sampled specimens. CB and PB sampled and sequenced fungi. SS analyzed the data and wrote the first draft of the manuscript. MMG, JM, CB, PB and ST contributed to improve later drafts.

Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting

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In fire-susceptible boreal forests, clear-cutting has been justified as being a harvesting regime that mimics natural stand-replacing dynamics, despite obvious differences in its biological legacies. Prescribed burning and retention forestry are commonly applied to better maintain naturally occurring legacies, but the community-level effects of different disturbances on the functional characteristics of biota remains still largely unknown. In this study, we investigated the effects of prescribed fire, clear-cutting and retention forestry on the functional properties of saproxylic beetle assemblages in Eastern Finland, using stand-level data from a before-after field experiment with four levels of tree retention (0, 10 and 50 m³ ha⁻¹ and control) and prescribed burning. We analyzed the functional-phylogenetic diversity and a set of species traits that link species to resources. Functional-phylogenetic diversity decreased from a random to a clustered pattern after burning and logging with retention trees, indicating environmental filtering of both processes. These effects became more pronounced with increasing logging intensity. Species-level traits that were favored by burning and tree retention were connected to open-habitat conditions and fresh dead wood, whereas clear-cutting revealed a random pattern without reference to specific resources. Our functional approach thus shows that clear-cutting does not mimic the dynamics of wildfire, but leads to different functional composition of species assemblages. Therefore, prescribed burning or wildfire should be incorporated and sufficient amount of trees retained in forest management to conserve functional processes and natural composition of saproxylic species assemblages in boreal forests.

JK, PM and OH developed and installed the experiment. PM and OH collected beetle data. SS and JM developed the idea, SS analyzed the data. SS and OH wrote the first draft of the manuscript and JK, MK, PM, ST and JM contributed to improve later drafts.

5 Discussion

Considering that human populations are increasing, the need for resources is likely to increase in future decades and with it the need for evidence-based and efficient strategies to reduce future loss of biodiversity and negative effects on ecosystem processes associated with it (Millennium Ecosystem Assessment 2005; Foley *et al.* 2005; Butchart, Walpole & Collen 2010; Hooper *et al.* 2012). With a significant portion of life in forest ecosystems being saproxylic or benefitting from dead wood, dead wood is one of the key structures for forest biodiversity (Speight 1989; Grove 2002). The role of these species in a number of critical ecosystem processes, e.g. wood decomposition, nutrient and carbon cycling, adds a further dimension and underlines the importance of dead wood and the species living in it (Hooper *et al.* 2012; Ulyshen 2014). To develop and further improve conservation strategies, the relation between species and the environment as well as the effects of human activities have to be well understood.

The objective of this thesis was to contribute to our understanding of such relations between saproxylic insects, environmental factors and human activities in temperate and boreal forests to derive recommendations for their conservation. As a first approach, the analysis of the extinction risk of saproxylic beetles in Western and Central Europe revealed that the red list status of species mirrors closely the ecological degradation of forests over the last centuries caused by modern forest management (Article 1). Particularly those species are more threatened that require resources which have become rare in managed forests. Forests management and conservation across all forests types in Central and Western Europe should thus focus on increasing the supply of these limiting resources. Here, adding dead wood is an effective measure as it positively affects saproxylic taxa and also non-saproxylic taxa worldwide, although the response of the later varied more strongly (Article 2). Reviewing the literature on experimental studies on dead-wood biodiversity revealed that experimental approaches complement our understanding of this topic and contributed strongly to conservation (Article 2). However, experimental studies have been concentrated in a few regions worldwide and certain functionally important and species-rich taxa as well as late decay stages have been rarely studied experimentally. Experimental manipulation of dead-wood amount and dead-wood diversity has revealed that habitat heterogeneity is the major driver of the diversity of saproxylic beetles and that microclimate has a strong mediating effect as determinant of the composition of beetle assemblages (Article 3). These results allow practical implications for conservation

strategies in forests in general and more specifically for temperate montane mixed forests which help to balance between ecologic and economic needs. Added dead wood is readily colonized also by threatened saproxylic insects, such as saproxylic heteropterans (Article 4). To locate such new resources on longer distances, saproxylic heteropterans are more attracted by dead wood itself than by their fungal hosts. In boreal forests, the functional composition of saproxylic beetle assemblages differs strongly between clear-cuts and forests subject to prescribed burning and retention forestry and thus, clear-cutting does not mimic natural disturbances (Article 5). Instead, retaining differing amounts of trees and applying prescribed burning in some forest stands can help to maintain a high diversity of saproxylic beetles in managed forests on the landscape level.

5.1 Patterns of extinction risk of saproxylic beetles in Europe

Linking the red list status of species to biological and habitat related species' traits allows identifying the major drivers of extinction over large regions and across a wide range of habitats (Fritz, Bininda-Emonds & Purvis 2009; Cardillo & Meijaard 2012; Di Marco *et al.* 2014). The climate and the history of forest management of Germany are comparable with those of surrounding countries and thus, results of the analysis of the German red list of saproxylic beetles (Schmidl & Büche 2015) should be broadly transferable to Central and Western Europe. While accounting for the ordinal nature of the response variable and the relatedness of species by including species-specific random intercepts based on the phylogeny, the modeling approach revealed higher extinction risk of species with a small range, lowland species and large-bodied species (Article 1). With regard to resources, species requiring dead wood of large diameter, dead wood of broad-leaved tree species and sun-exposed dead wood were more prone to extinction. This pattern can be traced back to the major changes in forests of the study area over the last centuries. Lowland forests are among the most heavily reduced and altered forest types in Europe (Klimo & Hager 2000; Larsson 2001; Whitehouse 2006), whereas in mountainous terrain more near-natural forest remained with generally higher dead-wood volumes (Scheifele 1988; Thünen-Institut für Waldökosysteme 2014). Starting in the early 19th century (Hartig 1808), dead wood and old-growth trees were removed from forests as part of a strategy of “forests hygiene” and harvesting has prevented trees from reaching natural senescence. Dead wood of large diameter is therefore particularly rare (Thünen-Institut für Waldökosysteme 2014) and with it, saproxylic beetle species that prefer such large-diameter dead wood and large species that need dead wood of a minimum size to fulfill larval development (Foit 2010). To fulfill

demands for timber, conifer species were planted at the expense of naturally dominant broad-leaved tree species in most European countries beginning in the early 19th century (Dirkx 1998; Radkau 2007). At the same time, multi-use systems including coppicing and forest pasture ceased and formerly open and sunny forests transformed to dense and dark high forests characterized by high growing stock (Schelhaas, Nabuurs & Schuck 2003; Radkau 2007). Dead wood in such production forests is thus rarely sun exposed (Larsson 2001), particularly as dead wood created by natural disturbances which simultaneously open the canopy is frequently salvage logged (Lindenmayer *et al.* 2004).

5.2 Knowledge gaps regarding biodiversity in dead wood

Realizing the tremendous loss of dead wood as habitat and the decline of many saproxylic species, researchers started to evaluate the relationship between biodiversity and dead wood some decades ago. As field surveys not always allow revealing causalities, experimental approaches have been pursued at an accelerating rate. A review of published literature complemented with unpublished studies by approaching experts from several countries resulted in a list of 79 experimental studies focusing on biodiversity patterns in dead wood worldwide (Article 2). Categorization of these studies according to biome, manipulated factors and studied species groups revealed that research is biased towards temperate and boreal forests of Europe, North America and Australia, towards saproxylic beetles and vertebrates and early decay stages. Many studies focused only on one species group and are thus not used to their full potential. In particular, several species-rich and functionally important taxa such as wood-decaying fungi, Diptera and termites or taxa of conservation concern such as bryophytes and lichens are under-represented in experimental dead-wood studies. As species richness of some of these taxa peak at later decay stages and most studies followed only the first years of succession, these taxa would benefit from studies focusing on late stages of wood decomposition. Instead of starting new experiments, existing experimental set-ups could be revisited to study such late-successional species. To allow researchers to identify suitable experiments, a map and a list of existing set-ups including information on the date of start, manipulated factors and studied taxa is provided. Furthermore, sequencing of fungal DNA from wood samples has become available which detects more species already at earlier successional stages than traditional fruit body surveys and could thus complement traditional techniques (Ovaskainen *et al.* 2013). Similarly, methods like DNA barcoding (Schindel & Miller 2005) can help to identify cryptic taxa such as dipterans and thus, allow researchers to focus also on these largely

neglected species groups. A variety of different dead-wood factors were studied experimentally, most frequently dead-wood amount, forest management and differences between tree species. The meta-analysis of the effects of dead-wood addition revealed a consistently positive response of saproxylic taxa worldwide to dead-wood addition and an overall positive but more heterogeneous response of non-saproxylic taxa (Article 2). This highlights the importance of this measure as a means to conserve taxa associated with dead wood as well as of strategies that target at reaching minimum thresholds of dead-wood volume (Müller & Bütler 2010). Recently, several studies have demonstrated that interactions between different factors, such as dead-wood amount and temperature (Müller *et al.* 2015c), but also between different taxa as indicated e.g. by priority effects (Fukami *et al.* 2010; Weslien *et al.* 2011), are important for conservation of saproxylic species and ecosystem functioning. Future studies should therefore focus on disentangling such interactions by pursuing experimental approaches.

5.3 Disentangling the role of dead-wood amount and dead-wood diversity

The Bavarian Forest Dead-wood Experiment focused on such a potentially important interaction namely between dead-wood amount and dead-wood diversity (Article 3). It revealed that both dead-wood amount and dead-wood diversity affected the species richness of saproxylic beetles independently. While the effect of dead-wood diversity supported the habitat-heterogeneity hypothesis, the increasing number of species with dead-wood amount was not in line with the more-individuals hypothesis (species-energy hypothesis) as it was not caused by an increase in abundance, but was a direct effect. One possible explanation here is cryptic variation of factors, e.g., temperature, moisture, fungal colonization or wood density, which vary within single dead-wood objects, particularly when of large size, and which thus cannot be manipulated (e.g., Graham 1924; Saint-Germain, Buddle & Drapeau 2010; Leather *et al.* 2014). The positive effect of dead-wood amount may thus also be caused by an increase in niche diversity with increasing amount of dead wood of the same type. This indicates that the effects of both dead-wood amount and dead-wood diversity on richness of saproxylic beetles can be attributed to habitat heterogeneity rather than resource availability.

Canopy openness also strongly affected saproxylic species assemblages with generally higher abundance and more species in sunny forests. This can be partly caused

by increasing activity of insects with increasing temperature (Liu, Zhang & Zhu 1995; Beudert *et al.* 2015) which affects activity traps like flight-interception traps (Wikars, Sahlin & Ranius 2005; Alinvi *et al.* 2006). However, temperature affects not only the activity of insects but also the rate of physiological processes (Clarke & Gaston 2006), with e.g. shorter development phases under warmer conditions (Schowalter 2006). Thus, an increase in the abundance of insects with increasing temperature can be expected. This expectation was confirmed by the results described in the third article as well as by rearing experiments of dead wood exposed in warm and cold climate (Vodka, Konvicka & Cizek 2008; Müller *et al.* 2015a). Furthermore, ordination of species assemblages, indicator analysis and a marginally significant effect of microclimate on species richness of saproxylic beetles indicated that the species composition differed strongly between sunny and shady forest plots. For instance, temperature variability and maxima inside dead wood were higher on sunny than shady plots which may preclude species sensitive to high temperatures (Graham 1924). In European temperate montane mixed forests, specialists of broad-leaved dead wood were more abundant in shady conditions while conifer-specialists and generalists preferred sunny plots. This indicates that host specificity of saproxylic beetles may interact with their preferences for microclimatic conditions (Müller *et al.* 2015a).

The effects of dead-wood amount and dead-wood diversity were also mediated by microclimate as dead-wood amount was more important in sunny conditions and dead-wood diversity prevailed in shady forests. The weak effect of dead-wood diversity in sunny habitats may be due to lower colonization of branches on sunny plots, as observed when beetles were reared from branch samples from sunny and shady plots. In turn, the stronger effect of dead-wood amount on sunny plots may be caused by a higher spatial variability of dead-wood quality within logs when partly exposed to strong solar radiation, i.e. having a dry and warm upper part and a cool and moist lower part (Graham 1924). Thus, the effect of dead-wood amount on sunny plots may have been also caused by higher habitat heterogeneity with increasing amount of dead wood.

5.4 How saproxylic insects locate new resources

Exposed dead wood of the Bavarian Forest Dead-wood Experiment was readily colonized by saproxylic heteropterans, mostly of the family Aradidae (Article 4). The abundance of heteropterans was higher on sunny than shady forest plots. This might be partly caused by higher activity rates in warm habitats but is in line with published habitat preferences of

the sampled species (Gossner, Engel & Blaschke 2007; Heiss & Pericart 2007; Wachmann, Melber & Deckert 2007) – with one exception (*Aradus depressus*) which was more abundant on shady plots – and might thus represent true differences in population sizes. Although saproxylic heteropterans forage on tissue, particularly mycelia, of certain fungal hosts (Heiss & Pericart 2007), the amount of dead wood of large diameter was the major driver of their abundance. Neither the abundance of all fungal species nor of fungal host species only – measured as the number of fruit bodies per sector (1 m long section of a dead-wood object) – affected the abundance of saproxylic heteropterans.

In general, the overall profile of volatile chemicals emitted from dead wood changes during the decomposition process (Holighaus & Schütz 2006) and depends on both wood characteristics and the fungal community colonizing the log (Leather *et al.* 2014). Saproxylic insects are able to differentiate between these different profiles to locate new habitat patches (Fäldt *et al.* 1999; Weissbecker, Holighaus & Schütz 2004). As emitted chemicals are mostly wood-borne during the first two years after a tree dies (Holighaus & Schütz 2006), the observed attraction of saproxylic heteropterans to dead wood of large diameter suggests that these species use wood-borne chemical volatiles instead of chemicals emitted by fungal species to locate new resources at least during the early succession. The attracting effect of dead wood may increase with its amount as the amount of emitted chemicals increases with increasing surface area (Rasmussen 1972).

However, the type and source of cues to locate a suitable resource might differ between spatial scales (Saint-Germain, Buddle & Drapeau 2007, 2010). Parasitoid beetles, for instance, use volatile chemicals emitted by the preferred feeding plant of its host for long-distance orientation but volatile chemicals emitted by its host for short-distance orientation (Goubert *et al.* 2013). It is thus possible that saproxylic heteropterans are primarily attracted by dead wood but use different sources of volatile chemicals or other cues to evaluate the suitability of a log, e.g. the presence of a certain host fungi, in a second phase after landing. The abundance of wood-decaying fungi was assessed as the number of fruit bodies in log sections of 1 m length. Thus, saproxylic heteropterans might have responded to volatile chemicals emitted by mycelia of fungal host species that are already present in the dead wood but have not yet formed fruit bodies. However, genetic analyses of 93 drilled core samples taken from the same dead-wood objects showed that the proportion of potential host mycelia in relation to all fungal species was low (3.9%; Bässler & Baldrian, unpublished data), similar to that found for fruit bodies (2.9%). Thus, the occurrence of potential host fungi was not underestimated by our fruit body survey.

5.5 Effects of clear-cutting, fire and tree retention

Earlier analyses of species richness pattern of data of the FIRE-Experiment showed that clear cuts host less saproxylic beetles species than forest stands subject to prescribed burning or when green trees were retained, particularly of rare and red-listed species (Hyvärinen *et al.* 2005; Hyvärinen, Kouki & Martikainen 2006). The trait-based approach now revealed that the treatments led not only to differences in species richness but were accompanied by shifts in the composition of beetle assemblages with regard to body size, feeding strategy and preferences for decay stage and sun exposure of the required dead wood (Article 5).

Fire kills most of the original insect populations (McCullough, Werner & Neumann 1998) and enables the colonization of species that have enabled to rapidly colonize new resources (Wikars 1997; Boulanger & Sirois 2007). The post-fire environment is characterized by microclimate of open-canopy forests with less shady conditions and high amounts of freshly dead or dying trees damaged by the fire (Moretti *et al.* 2010; Heikkala *et al.* 2014). As expected with regard to these habitat changes, saproxylic beetle assemblages after burning were dominated by specialists of early decay stages and sunny habitats. Species that feed on fresh dead wood increased and also predators increased after fire, probably due to higher prey availability. Fire also led to an increase in late-stage xylophagous species, possibly because fire accelerates the decomposition process by partly consuming phloem and cambium, hence opening niches for xylem specialists. Overall, with regard to species' traits and considering phylogenetic relationships, post-fire beetle assemblages showed a clearly clumped community structure.

Harvesting with tree retention opens the canopy creating sunny habitat conditions and increases the amount of fresh dead wood as many retention trees in the studied stands are wind-blown or die standing soon after logging (Heikkala *et al.* 2014). Saproxylic beetle assemblages in these stands were also clumped with regard to species traits and phylogeny and particularly dominated by species that require sunny conditions and dead wood of early decay stages, such as bark beetles. This pattern was more pronounced when fewer trees were retained indicating that at higher retention levels, there is a broader spectrum of resources. This is supported by less negative effects of cutting with 50 m³ ha⁻¹ retention on late-stage xylophagous and mycetophagous species than at the 10 m³ ha⁻¹ level. In contrast to the expectation that large species which require mostly larger dead-wood objects (Foit 2010; Bussler *et al.* 2011) are less abundant after harvesting as trunks are removed while

many small species benefit from the increased abundance of slash, the mean body size of beetle assemblages increased with harvesting intensity. This shift in mean body size was not caused by a loss of large species but of small species indicating that post-harvest resources were less abundant for small species than for large species. At higher retention levels, standing dead trees provide high amounts of branch material suspended over ground, while at low retention levels more branches are transferred to the ground (Heikkala *et al.* 2014). Differences in microclimatic conditions may affect the suitability of this substrate (Thorn *et al.* 2014) and therefore, the available amount of suitable resources for small species may actually decrease with increasing harvesting intensity.

Saproxylic beetle assemblages after clear-cutting showed no clumped but a random community structure with regard to species' traits and phylogeny. Both feeders of early and late-stage xylophagous species increased and no strong dominance of light-demanding species was observed. Analyses of species assemblage characteristics thus revealed that burned stands and harvested stands with retention trees host specific beetle assemblages adapted to the characteristic combination of resources and microclimate created by fire or the opening of forests. Clear-cuts, in contrast, host assemblages which consist of a "random" combination of species and thus, do not mimic conditions of natural stand-replacing dynamics such as fires. However, differences in the functional and phylogenetic composition of saproxylic beetle assemblages after the different treatments do not necessarily indicate that ecosystem functions in which saproxylic beetles are involved are affected by harvesting. Our knowledge of the role of biodiversity and functional properties of saproxylic communities for ecosystem functioning is still rudimentary and should be improved in further studies (see 5.7).

5.6 Implications for the conservation of saproxylic species

One of the major objectives of this thesis was to derive implications to improve conservation strategies for saproxylic species. Each article therefore ended with a number of recommendations based on its results which ranged in spatial scope from a global perspective to a focus on temperate or boreal forests, or a particular focus on temperate montane mixed forests in Europe. Recommended targets and measures can be applied in protected areas as well as in production forests and can guide both practitioners and political decision makers who decide upon financial incentives for conservation in private forest or conservation targets for state forests.

- Target 1: Microclimate is a major determinant of species composition of saproxylic insects. Dead wood should therefore be provided along the full range of canopy openness including extreme sunny and shady conditions. In Central and Western Europe, dead wood in sunny conditions is rarer than in shady conditions and should therefore be increased across all types of forest by intentional accumulation in gaps, cutting of shading trees neighboring habitat trees, or benign neglect after natural disturbances.
- Target 2: Habitat heterogeneity is the major driver of saproxylic beetle diversity and should be maintained or directly or indirectly increased in all forest ecosystems.
- a) Dead-wood diversity can be actively increased, e.g. by selectively and repeatedly creating dead wood of less abundant local tree species and of large diameters. In Central and Western Europe, particularly the amount of broad-leaved dead wood and dead wood of large diameter should be increased.
 - b) Dead-wood amount is a good proxy for habitat heterogeneity. Thus, high habitat heterogeneity can be achieved indirectly by aiming at reaching proposed thresholds of dead-wood amount (Müller & Bütler 2010).
 - c) Specifically for temperate montane mixed forests in Europe, dead-wood diversity should be increased in shady forests and dead-wood amount in sunny forests.
- Target 3: Increasing the amount of dead wood by cutting, girdling, topping, burning or other methods have shown to provide habitat for rare and threatened saproxylic species and increase biodiversity worldwide. Such active measures of dead-wood enrichment should therefore complement the retention of natural dead wood.
- Target 4: In Central and Western Europe, lowland forests should be set aside for conservation rather than forests on remote mountains.
- Target 5: In boreal forests, different amounts of green trees should be retained during harvesting and prescribed burning of selected stands or benign neglect towards wildfire should be applied to obtain a mosaic of stands in different early

successional stages alongside mature forests that host a wide range of saproxylic beetle assemblages.

5.7 Future directions

Besides gaps in knowledge of how environmental and anthropogenic factors affect biodiversity patterns of species related to dead wood (section 5.2), our understanding of the role of dead-wood biodiversity for ecosystem processes and functioning is particularly rudimentary. Such knowledge, however, is crucial in various ways: 1) the accuracy of models of ecosystem processes and services can be increased by including effects of organisms (Bradford *et al.* 2014); 2) the effects of biodiversity loss on ecosystem processes and services can be evaluated (Cardinale *et al.* 2012; Hooper *et al.* 2012); 3) conservation strategies can be developed to consider both biodiversity and ecosystem functioning (Devictor *et al.* 2010); 4) quantifying the role of biodiversity for ecosystem services may help to increase conservation efforts (Balvanera *et al.* 2006).

The probably most important process in which saproxylic taxa are involved is the decomposition of dead wood – a key process in nutrient and carbon cycling (Hooper *et al.* 2012; Ulyshen 2014). Researchers have started to quantify the contribution of different taxonomic groups, e.g. saproxylic insects or fungi, to wood decomposition (Fukami *et al.* 2010; Ulyshen 2014) but effects vary biogeographically (Tedersoo *et al.* 2014) and particularly relative to climate (Wall *et al.* 2008), and thus, no global pattern could be revealed for wood decomposers yet (Ulyshen 2014). Besides the general role of different taxonomic groups, specific characteristics of assemblages may be important. For instance the functional composition may be more important than species richness (Heemsbergen *et al.* 2004) but no uniform relationship between decomposition rates and decomposer diversity has been demonstrated to date (van der Wal *et al.* 2013). A promising approach, e.g., would be to manipulate saproxylic assemblages to form gradients of species richness and functional diversity and measure the effects of both factors on wood decomposition rates. Furthermore, integrating species' traits like body size or feeding strategies into such experiments would allow predictions how effects of management on functional characteristics of assemblages as described in section 5.5 would affect decomposition rates.

Interactions between species or groups of higher taxonomical level can affect the colonization of dead wood and also its decomposition. The arrival order of fungal colonists in wood, e.g., caused differences in fungal species richness and decay rates of up to 300%

(Fukami *et al.* 2010). Furthermore, interactions of invertebrates with fungi or bacteria can affect microbial activity (A’Bear, Jones & Boddy 2014) or microbial community composition (Crowther *et al.* 2013). Saproxylic beetles have been shown to affect fungal communities by providing entries for airborne fungal spores or by vectoring of species (Persson *et al.* 2009; Persson, Ihrmark & Stenlid 2011; Strid *et al.* 2014). Here, associations of certain fungal and beetles species have been reported by field surveys (Müller *et al.* 2002; Weslien *et al.* 2011). For litter decomposing communities, it has been shown that such indirect effects via interaction with other species groups can even outweigh direct effects on decomposition rates (Hättenschwiler, Tiunov & Scheu 2005). Thus, interactions between different taxa and their effects on wood decomposition should be studied in more detail.

5.8 Conclusion

Deforestation and alteration of remaining forests has threatened and is still threatening species and ecosystem processes related to dead wood. In most regions worldwide, biodiversity of saproxylic species today depends on forest management and conservation. In Central and Western Europe, for instance, the red list status of saproxylic beetles mirrors closely the ecological degradation of forests caused by forest management over the last centuries. Conservation of threatened species should aim at increasing the amount of resources which are limiting populations – broad-leaved dead wood, dead wood of large diameter and sun-exposed dead wood – and at setting aside lowland forests for conservation. Furthermore, I showed that habitat heterogeneity is the major factor for saproxylic beetle diversity which should thus be increased or maintained. This can be achieved indirectly by increasing the amount of dead wood or directly by providing dead wood of different tree species and diameter classes. A meta-analysis of the effects of active dead-wood enrichment on biodiversity has proved it a meaningful complement to dead-wood retention for saproxylic and non-saproxylic taxa throughout the world. In boreal forests, the composition of saproxylic beetle assemblages based on species’ traits and phylogenetic relatedness differed between clear-cut, burned and harvested forest stands with retention trees. Clear-cutting thus does not mimic natural stand-replacing dynamics. Instead, various levels of green trees should be retained on the landscape level and selected stands should be subject to burning to maintain species communities of early-successional stages alongside with those of mature forests.

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Appendix I

Publication list

List of articles published in peer-reviewed and non-peer-reviewed journals during the time span of this thesis within the framework of dead-wood ecology or in a general ecological context.

Dead-wood ecology:

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D. & Müller, J. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*. Accepted.

Heikkala*, O., **Seibold***, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S. & Kouki, J. (2015) Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. *Forest Ecology and Management*, **359**, 51–58. doi: 10.1016/j.foreco.2015.09.043.

*Both authors contributed equally to this publication.

Seibold, S., Bässler, C., Brandl, R., Gossner, M. M., Thorn, S., Ulyshen, M. D. & Müller, J. (2015) Experimental studies of dead-wood biodiversity – A review identifying global gaps in knowledge. *Biological Conservation*, **191**, 139–149. doi: 10.1016/j.biocon.2015.06.006.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, **29**, 382–390. doi: 10.1111/cobi.12427.

Seibold, S., Bässler, C., Baldrian, P., Thorn, S., Müller, J. & Gossner, M. M. (2014) Wood resource and not fungi attract early-successional saproxylic species of Heteroptera - an experimental approach. *Insect Conservation and Diversity*, **7**, 533–542. doi: 10.1111/icad.12076.

Müller, J., Baier, R., Barimani, H., **Seibold, S.**, Talebi, K., Thorn, S. & Gossner, M.M. (2015) Protecting the forests while allowing removal of damaged trees may

ecologically degrade the Hyrcanian beech forests of Iran. *Conservation Letters*. doi: 10.1111/conl.12187.

Thorn, S., Bässler, C., Bußler, H., Lindenmayer, D.B., Schmidt, S., **Seibold, S.**, Wende, B. & Müller, J. (2016) Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. *Forest Ecology and Management*. In press.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M.W., Heibl, C., Schäfer, H., **Seibold, S.** & Müller, J. (2015) Changes in the dominant assembly mechanism drives species loss caused by declining resources. *Ecology Letters*. doi: 10.1111/ele.12548.

Thorn, S., Hacker, H., **Seibold, S.**, Jehl, H., Bässler, C. & Müller, J. (2015) Guild-specific response of forest Lepidoptera highlight conservation oriented forest management – implications from conifer dominated forests. *Forest Ecology and Management*, **337**, 41–47. doi: 10.1016/j.foreco.2014.10.031.

Thorn, S., Werner, S. A. B., Wohlfahrt, J., Bässler, C., **Seibold, S.**, Quillfeldt, P. & Müller, J. (2015). Response of bird assemblages to windstorm and salvage logging – Insights from analyses of functional guild and indicator species. *Ecological Indicators*. doi: 10.1016/j.ecolind.2015.06.033.

Winter, M.-B., Ammer, C., Baier, R., Donato, D., **Seibold, S.** & Müller, J. (2015) Multi-taxon alpha diversity following bark beetle disturbance: evaluating multi-decade persistence of a diverse early-seral phase. *Forest Ecology and Management*, **338**, 32–45. doi: 10.1016/j.foreco.2014.11.019.

General ecological topics:

Seibold, S., Buchner, J., Bässler, C. & Müller, J. (2013) Ponds in acidic mountains are more important for bats in providing drinking water than insect prey. *Journal of Zoology*, **290**, 302–308. doi: 10.1111/jzo.12041.

Seibold, S., Hempel, A., Piehl, S., Bässler, C., Brandl, R., Rösner, S. & Müller, J. (2013) Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. *Basic and Applied Ecology*, **14**, 687–693. doi: 10.1016/j.baae.2013.09.003.

Articles in non-peer-reviewed journals:

Seibold, S. & Leibl, F. (2015) Vier bundesweite Eckpfeiler gegen den Artenschwund bei Totholzbewohnern. *AFZ-Der Wald*, **8**, 23–24.

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Seibold, S., & Fischer, A. (2013) Suppression of alien invasive species by traditional land use forms: *Amorpha fruticosa* L. in the Croatian nature park Lonjsko Polje. *Sauteria*, **20**, 265–276.