



Review

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



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ABSTRACT

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 saproxyllic taxa, e.g., fungi, flies and termites, remain under-represented. Our meta-analysis confirms the benefits of dead-wood addition for biodiversity, particularly for saproxyllic taxa, but shows that responses of non-saproxyllic 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.

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1. Introduction

1.1. Biodiversity in dead wood

Accumulations of dead wood in forest ecosystems provide important resources for a wide range of organisms, including both saproxylic species, i.e., directly or indirectly dependent on dying or dead wood, and non-saproxylic species. Saproxylic species include a wide variety of wood-decaying fungi, which are one of the most diverse but least understood groups among saproxylic taxa (Boddy et al., 2008; Stokland et al., 2012); a large proportion of all forest arthropod species (Grove, 2002a; Speight, 1989) and cavity-nesting birds (McComb and Lindenmayer, 1999 and references therein). Non-saproxylic species include many small-bodied litter-dwelling invertebrates and vertebrates that use woody debris for shelter and nesting (Fauteux et al., 2012; Mac Nally et al., 2001) or that benefit from dead wood as a relatively stable source of moisture and a buffer against extreme temperatures (Ulyshen et al., 2011). Additionally, many epixylic lichens and bryophytes use dead wood as their habitat (Andersson and Hytteborn, 1991; Spribille et al., 2008) and tree seedlings on decayed logs and plants growing near dead wood benefit from recycled nutrients and microclimatic conditions (Szewczyk and Szewczyk, 1996).

1.2. Dead wood – patterns and determinants of resource availability

Species associated with dead wood are sensitive to the amount, variety and distribution of woody debris, which collectively determine the availability of accessible resources (Sverdrup-Thygeson et al., 2014b). Various abiotic and biotic factors, e.g., climate, soil type and diversity of woody plant species, interact across a wide range of scales, e.g., biome, landscape and forest stand to determine the abundance and variety of resources available to saproxylic organisms (Fig. 1; Müller et al., 2015; Stokland et al., 2012). Anthropogenic forces, such as extraction of fuel wood and timber, and conservation management represent the extremes of a gradient of forest-use intensity and also play important and sometimes dominant roles in influencing the amount, variety and distribution of woody debris across the landscape (e.g., Gossner et al., 2013b). The nature of wood removal varies around the world, ranging from large-scale industrial harvests to the informal collection of woody material by local populations for domestic use (Grainger, 1999; Ribot, 1999). These activities determine the amount of dead wood within forest stands as well as the type of dead wood, e.g., stumps in managed forests and snags in unmanaged forests (Christensen et al., 2005; Grainger, 1999). Moreover, dead wood features created by natural disturbances are, to an increasing degree, consciously influenced by human decision makers who decide whether to salvage harvest or not (Lindenmayer et al., 2004). Without human impact, natural disturbances strongly affect the temporal and spatial dynamics of forests and dead wood (Radeloff et al., 2000; Seidl et al., 2014) and create specific resource types, such as charred wood after fire or uprooted trees after windthrows, both of which host specialized saproxylic species (e.g., Hyvärinen et al., 2006; Menzel et al., 2003). To compensate for the lack of trees affected by wild fire in managed landscapes, prescribed burning is now regularly applied in many regions (Similä and Junninen, 2012).

An additional group of factors act not on areal units, but on individual trees or dead-wood objects (Fig. 1). Sun exposure, for instance,

affects microclimatic conditions and might strongly influence, in turn, the composition of saproxylic species assemblages (Bässler et al., 2010; Vodka et al., 2008). The composition of saproxylic assemblages is strongly determined by the type of dead wood as many species specialize on certain diameter classes, decay stages, vertical positions or tree species (Grove, 2002a; Heilmann-Clausen, 2001; Müller et al., 2015). Furthermore, many saproxylic species depend on the presence of other species as a resource or vector or for creating specific conditions in dead wood (Fukami et al., 2010; Strid et al., 2014). When dead wood develops naturally, the cause of death can be important. For example, a slow process of senescence creates different dead-wood substrates than a fast die-off and the different substrates thus host different saproxylic species assemblages (Ranius et al., 2009). Dead-wood snags created artificially, e.g., by using explosives, can be distinguished by some species from snags created naturally (Jonzell et al., 2004).

1.3. Dead-wood ecology in the context of ecological theories

Biodiversity patterns related to dead wood can be discussed in the context of a number of ecological theories. Patterns of species richness in relation to dead-wood amount, for instance, may follow mechanisms described by the *species-energy hypothesis* (Stokland et al., 2012; Wright, 1983) and effects of dead-wood diversity could be explained by the *habitat-heterogeneity hypothesis* (MacArthur and MacArthur, 1961). Habitat heterogeneity seems particularly important as effects of habitat heterogeneity peak at certain taxa-dependent spatial scales linked to keystone structures and dead wood represents such a keystone structure for saproxylic species (Tews et al., 2004). On larger spatial scales, habitat heterogeneity may be negatively perceived as fragmentation (Tews et al., 2004) and may become important when evaluating the spatial distribution of dead-wood substrates. The recently proposed *habitat-amount hypothesis* provides a synthesis of habitat size and isolation under the term “habitat amount”, which has to be experimentally determined for saproxylic organisms (Fahrig, 2013). Dead wood is an ephemeral resource and particularly in fragmented landscapes, spatial and temporal population dynamics of saproxylic species can be linked to the *theory of metapopulations* (Levins, 1969; Ranius et al., 2014). Following the *assembly theory* (Weiher and Keddy, 1995), environmental factors as well as the time of arrival of individual species during successive colonization of dead wood has strong effects on the composition of saproxylic assemblages (e.g. Bässler et al., 2014; Fukami et al., 2010). Furthermore, the *metabolic theory of ecology* (Allen et al., 2002) is a potentially important concept for dead-wood ecology and considers the effects of climate that have been shown to interact with dead-wood amount (Müller et al., 2014).

1.4. Acknowledging the importance of a resource under threat

Humans and organisms dependent on dead wood have competed for wood resources for thousands of years (Speight, 1989). Widespread forest clearance and the loss of old trees coupled with demands placed on remaining forest patches have dramatically reduced the amount and diversity of dead wood at a wide range of scales and throughout much of the world (Grove, 2002a; Lindenmayer et al., 2012; Siitonen, 2001). Over the past 20–30 years, hundreds of papers describing saproxylic communities in relation to the environment have been

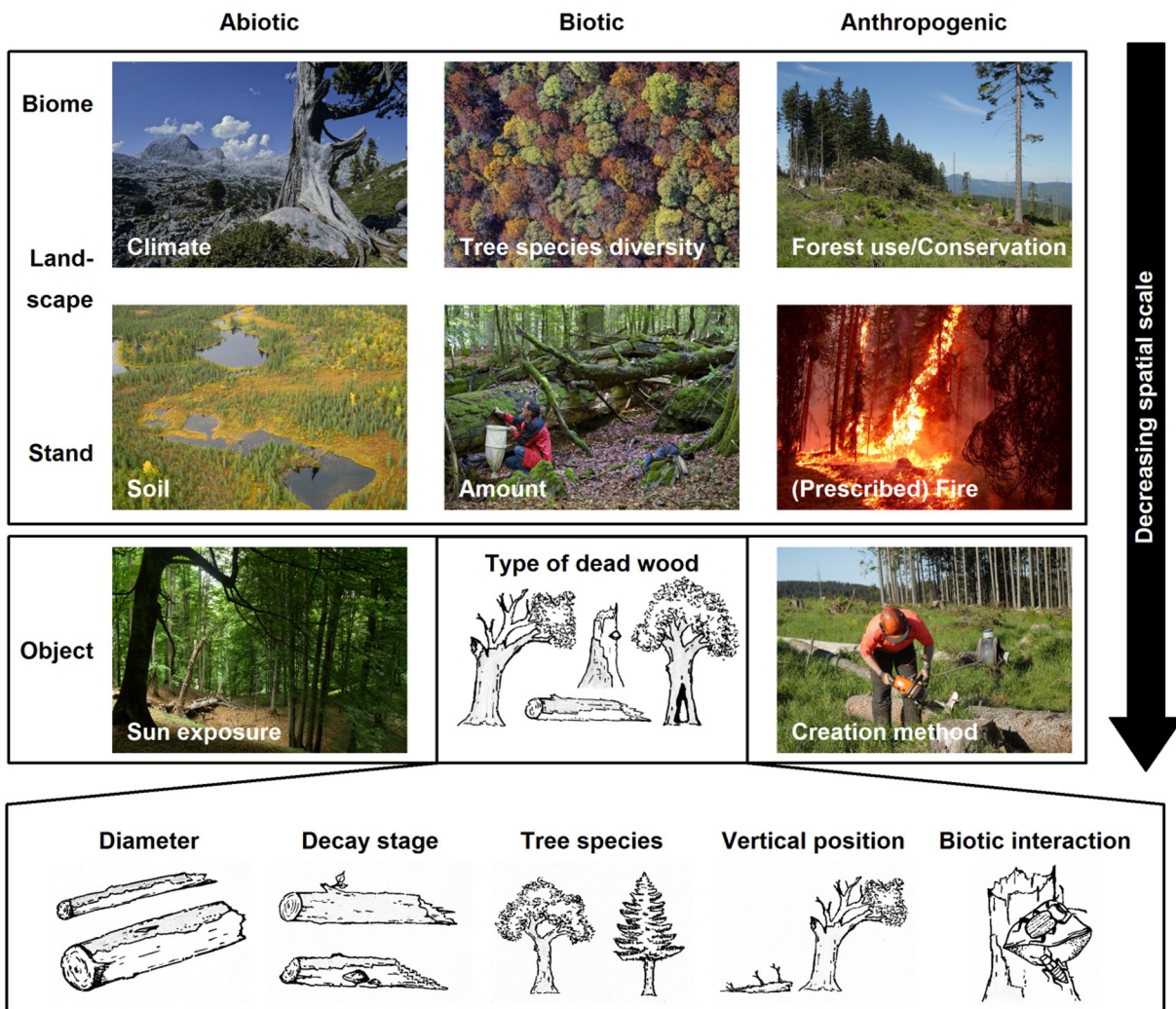


Fig. 1. Systematic list of factors affecting biodiversity in dead wood and manipulated in experimental studies of dead wood. The factors act on different spatial scales, ranging from the biome to stand level to a single dead-wood object. Note that fire is categorized as anthropogenic as most burned wood increasingly arises from prescribed burning and most burned wood from a wildfire is removed by salvaging. Photograph (fire) by Jari Kouki.

published and reviewed from different perspectives demonstrating the linkage between losses of dead wood and declines in biodiversity (Bouget et al., 2012; Davies et al., 2007; Grove, 2002a; Lassauce et al., 2011; Müller and Bütler, 2010; Siitonen, 2001; Stokland et al., 2012). For example, in Central and Western Europe, the extinction risk of saproxylic beetles clearly mirrors the ecological degradation of forests over the last centuries through forest management (Seibold et al., 2015). The studies provided insights into habitat preferences of saproxylic organisms and interactions within communities, demonstrated the sensitivity of many species to certain management activities and derived implications for their conservation (e.g., Bässler et al., 2014; Gossner et al., 2013b; Stokland et al., 2012). Because of these achievements, 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. However, such efforts have been largely restricted to boreal and temperate forests (e.g., Similä and Junninen, 2012) whereas few studies have focused on dead wood in tropical forests. Thus, conservation strategies for tropical forests remain poorly developed despite the many threats facing saproxylic organisms in these regions, e.g., the conversion of natural forests to arable land or plantations, fragmentation, and the selective logging of old trees (Grove, 2002b; Lachat et al., 2006; Lindenmayer et al., 2012).

1.5. Why experimental studies are needed

Because 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) given the associated costs and commitments, observational approaches are often necessary (Stephens et al., 2015) and serve as the basis for many existing saproxylic conservation strategies. Although these studies have been of great importance for conservation, causality of observed relationships are difficult to prove because of many possible confounding factors, such as differences in dead-wood type, age or management history among the studied stands. For example, a large proportion of studies have compared species assemblages among forests with different amounts of dead wood and many of these have shown positive relationships between dead-wood quantity and biodiversity (Junninen and Komonen, 2011; Müller and Bütler, 2010). This positive relationship can be explained either by the *species-energy hypothesis*, which predicts increasing species richness with increasing resource availability, or by the *habitat-heterogeneity hypothesis*. Dead-wood quantity is, however, correlated with dead-wood diversity (Müller and Bütler, 2010). Thus, field-survey data alone cannot determine whether the positive effect of high amounts of dead wood is caused by resource availability or by an increasing number of dead-wood substrates (Müller et al., 2010).

This example demonstrates the complexity behind observed biodiversity patterns and the need for multiple-scale experimental manipulations to reveal causalities (Davies et al., 2007). Clear standardized conditions and well-designed manipulations can distinguish between the effects of different factors on species assembly and ecosystem processes. Researchers have increasingly applied experimental approaches 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, as, for example, in boreal forests (Halme et al., 2013; Similä and Junninen, 2012). Importantly, the results from such experiments can be broadly generalizable when linked to general ecological theories.

Here we review both published and unpublished experimental field studies that focus on dead wood and biodiversity with the aim of providing recommendations for future experimental research. We summarize the results of experimental studies of dead wood for researchers, forest managers, and conservationists to complement existing reviews of observational studies (Davies et al., 2007; Grove, 2002a; Lassaue et al., 2011; Siitonen, 2001; Stokland et al., 2012). We furthermore list which research questions have already been addressed in the four main climate zones of the world that contain forest and which influencing factors and species groups have already been studied experimentally. With a focus on experimental studies, we aim at identifying gaps in knowledge on which future experiments should concentrate. We complement this with a meta-analysis of the effects of dead-wood addition on species richness based on experimental studies.

2. Methods

2.1. Literature review

To compile information on dead-wood experimental studies, we used a search string consisting of the subject “forest AND (woody\$material OR woody\$biomass OR high\$stump OR snag OR woody\$debris OR dead\$wood OR CWD OR FWD)” and the intervention “accumulat* OR experiment* OR manipula* OR creat* OR artificial OR girdl*” and contained wildcards where necessary (Pullin and Stewart, 2006). We refrained from including an outcome since our main focus was a summary of different experimental approaches. The search was conducted in April 2014 and updated on 9 November 2014; the following databases were searched: ISI Web of Knowledge, JSTOR, Science Direct, Directory of Open-Access Journals, CAB Abstracts, Scopus and GeoRef. These searches identified 1267 publications, which were first filtered by title (257), then by abstract (97) and finally by reading the full text. This list was supplemented by examining references of these articles for additional publications. To include running experiments that were not yet published, we approached experts from the global dead-wood ecology community to complement our obtained list of experimental field studies.

We included only experimental field studies conducted in terrestrial ecosystems that focused on biodiversity patterns, either on abundance, species number, species composition or functional composition. We considered studies as experimental when either the amount or diversity of dead wood was manipulated by exposure or creation in situ by, e.g., topping, girdling, cutting or burning. We also considered studies as experimental if manipulations were conducted during regular management activities, as long as pre-treatment conditions and manipulations resulted in highly standardized conditions. Exposed wood had to be at least 30 cm long. Studies that removed dead wood, e.g., by salvage logging, were not considered experimental as the amount and diversity of dead wood were not standardized before the treatments and thus the intensity of the treatments might have differed.

For all studies meeting these criteria, we categorized the manipulated factors, location and target species groups. Manipulated factors were classified as abiotic (microclimate/soil and sun exposure), biotic (tree species diversity, amount, diameter, decay stage, tree species and type

of dead wood, e.g., log, top, snag, stump, cavity, standing/downed, vertical position, horizontal distribution or biotic interaction), or anthropogenic (forest use/conservation, method of dead wood creation and prescribed burning; Fig. 1). Because we decided to group ants with termites as social insects, the target species group Diptera/Hymenoptera did not include ants. As all experiments studying forest use focused on systems of formal forest management and none on informal forms of wood collection, we use the term “management” when referring to forest use and protection status. We also evaluated whether publications were management-oriented and whether they tested ecological theories.

2.2. Meta-analysis and summary of reviewed studies

Dead-wood amount was the only factor that was studied frequently enough and with comparable experimental designs to conduct a meta-analysis. For each study that manipulated dead-wood amount, we 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. Data were extracted directly from published text or tables or from graphs using PLOT DIGITIZER 2.6.2 (www.plotdigitizer.sourceforge.net); we contacted authors to provide data if necessary. We extracted information on the number of plots, studied species group and time since addition of dead wood. We allowed multiple entries per experiment when multiple taxonomical groups were studied; when dead wood was placed under different conditions, such as open and closed forest; or when the effect of the treatment was studied for more than one year. Nested designs were handled as described below.

All analyses were conducted in R 3.0.2 (www.r-project.org) using the add-on package metafor for meta-analysis (Viechtbauer, 2010). We calculated Hedges' *d* standardized effect size (Hedges and Olkin, 1985) for comparing dead-wood addition and the control; Hedges' *d* accounts for small sample sizes and for differences in sampling effort across studies. 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). We modeled Hedges' *d* by applying 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, we included experiment as a random effect in the model.

For all other dead-wood factors, methodological differences and the number of studies precluded meta-analyses. Instead, we summarized the results in a quantitative head-count table of responses separately for species assemblages and numeric metrics, i.e., abundance, species richness, density and diversity. For numeric metrics, we counted the number of publications that reported a positive, negative or non-significant response if the dead-wood factor was numeric. For categorical dead-wood factors, such as tree species or dead-wood type, we counted the number of significant and non-significant numeric differences. We counted an effect as significant when at least one category differed significantly from others. Similarly, we counted the number of publications that reported significant and non-significant changes in species assemblages. When a study reported contradictory findings for different taxa without an overall result, the study was excluded.

3. Results

3.1. Overview of experimental studies

Our search resulted in 79 independent experimental studies from 23 different countries (Fig. 2; see Appendix for complete list and

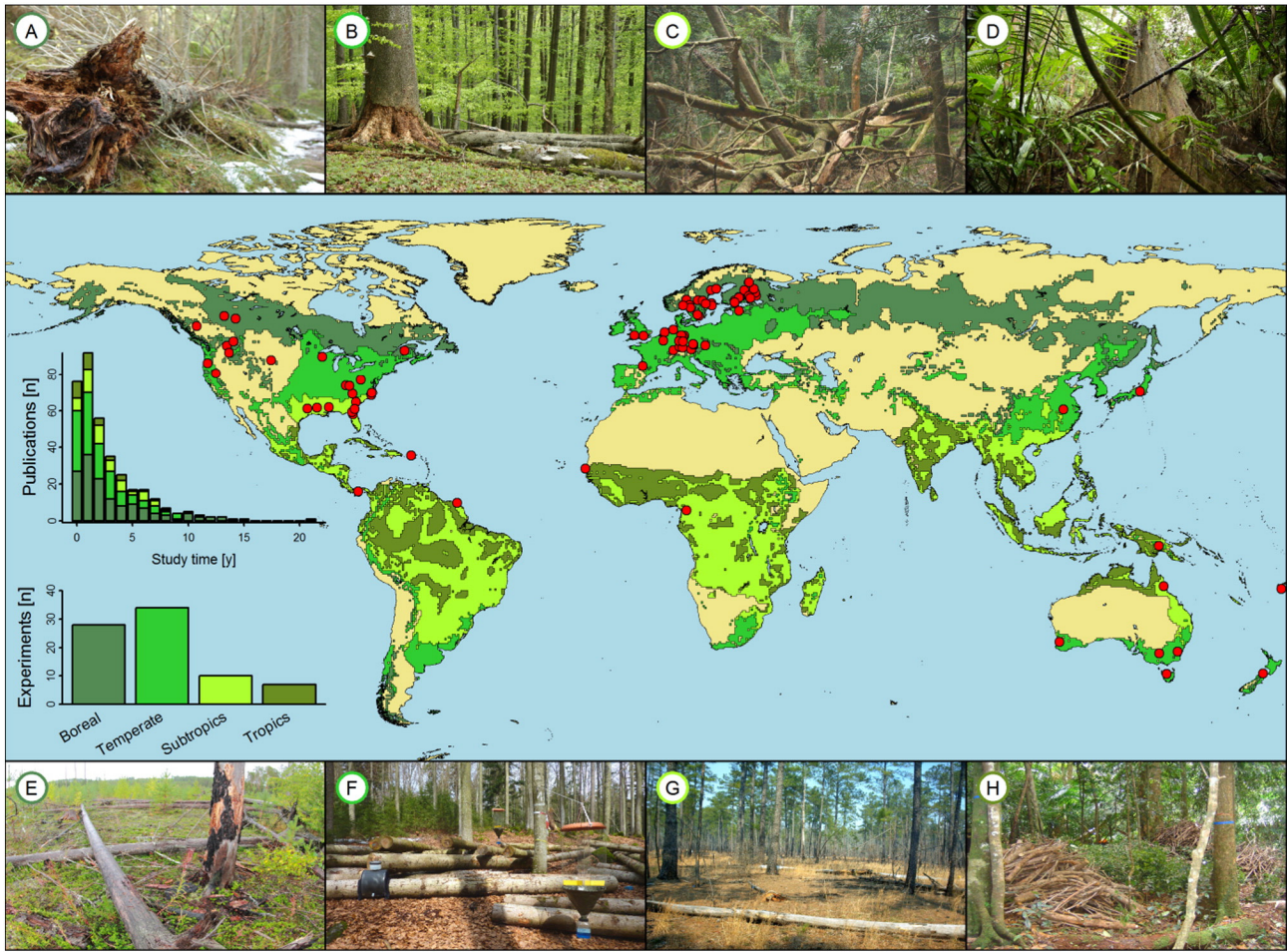


Fig. 2. Location of 79 experimental studies of dead wood (red circles) in each of the four forest biomes indicated by green shading (Holdridge, 1967; www.fao.org). Histograms show the number of experimental studies per biome (lower graph) and study duration, i.e., the number of publications reporting results for each year after the start of an experiment (upper graph). Photographs show typical examples of natural dead-wood habitats (upper row; A–D boreal, temperate, subtropical, tropical) and examples of experimental studies of dead wood in each biome (lower row; E, boreal, [Hyvärinen et al., 2006](#); F, temperate, [Seibold et al., 2014](#); G, subtropical, [Ulyshen and Hanula, 2009a](#); and H, tropical, [Schowalter et al., 2014](#)). Photographs: (G) Scott Horn, (H) Timothy D. Schowalter, (others) S. Thorn and S. Seibold.

references). The largest number of experimental studies were conducted in the temperate zone (36), followed by boreal zone (29), subtropical zone (9) and tropical zone (5) (Fig. 2, lower inset). Most studies focused on saproxylic beetles (51), followed by fungi (21), birds (12) and epigeic invertebrates (10), such as spiders, ground beetles or molluscs (Fig. 3). Six or fewer experimental studies examined small mammals, reptiles/amphibians, other invertebrates, e.g., dipterans, hymenopterans or heteropterans, lichens, bryophytes or vascular plants. Three studies recorded non-saproxylic beetles, bacteria or ants/termites. Two-thirds (66%) of all experiments studies recorded only one species group (Fig. 3, inset). The sampling frequency was highest during the first three years after the start of an experiment and then decreased steadily (Fig. 2, upper inset). Only a few studies followed long-term succession of experimentally added dead wood (e.g., [Hövmeyer and Schauer mann, 2003](#); [Penttilä et al., 2013](#)). The majority of publications (68%) were management-oriented and evaluated specific conservation or forest management strategies. Only 7% of all publications tested hypotheses based on general ecological theories, mostly derived from the *species-energy hypothesis* (Table A1).

Abiotic factors were studied in particular on the object level (Fig. 3) by shading single logs ([Hjältén et al., 2007](#)) or exposing dead wood on both shady and sunny forest plots ([Seibold et al., 2014](#)). On the landscape level, soil conditions were the focus of a few studies (e.g., [Cornelissen et al., 2012](#)), but macroclimate was only rarely examined (e.g., [Müller et al., 2014](#)). Of the biotic features of dead wood, the

amount of dead wood was most frequently manipulated in all climate zones, for example by exposing different numbers of logs ([Manning et al., 2013](#)) or by cutting, topping or girdling different numbers of trees (e.g., [Kroll et al., 2012](#); [Ulyshen and Hanula, 2009b](#)). Only six or fewer studies manipulated the horizontal distribution of snags ([Walter and Maguire, 2005](#)) or logs ([Barton et al., 2011](#)) or tree species diversity ([Seibold et al., 2014](#)). On the object level, tree species was most frequently studied, e.g., by comparing colonization of logs of different tree species ([Müller et al., 2015](#); [Tavakilian et al., 1997](#)). Differences between types of dead wood, such as stump, log, snag or top, and biodiversity were frequently studied, particularly in the boreal zone (e.g., [Hammond et al., 2001](#)). A few of these studies compared downed and standing dead wood (e.g., [Gibb et al., 2006b](#); [Ulyshen and Hanula, 2009a](#)), but an evaluation of the difference between downed and standing dead wood was not always possible because of confounding factors. For example, when the downed log was cut from the upper part of the trunk of the same tree that was topped, the resulting snag and log differed in diameter (e.g., [Fossestol and Sverdrup-Thygeson, 2009](#)). An intermediate number of studies focused on dead-wood diameter (e.g., [Grove and Forster, 2011](#)), decay stage ([Hövmeyer and Schauer mann, 2003](#)), or vertical position (e.g., [Gossner et al., 2013a](#)), or on biotic interactions between, e.g., fungi and beetles ([Strid et al., 2014](#)). Management was one of the two most frequently studied factors, either conservation-orientated (protected forests) or forest management for timber production. No experiment studied effects of extraction

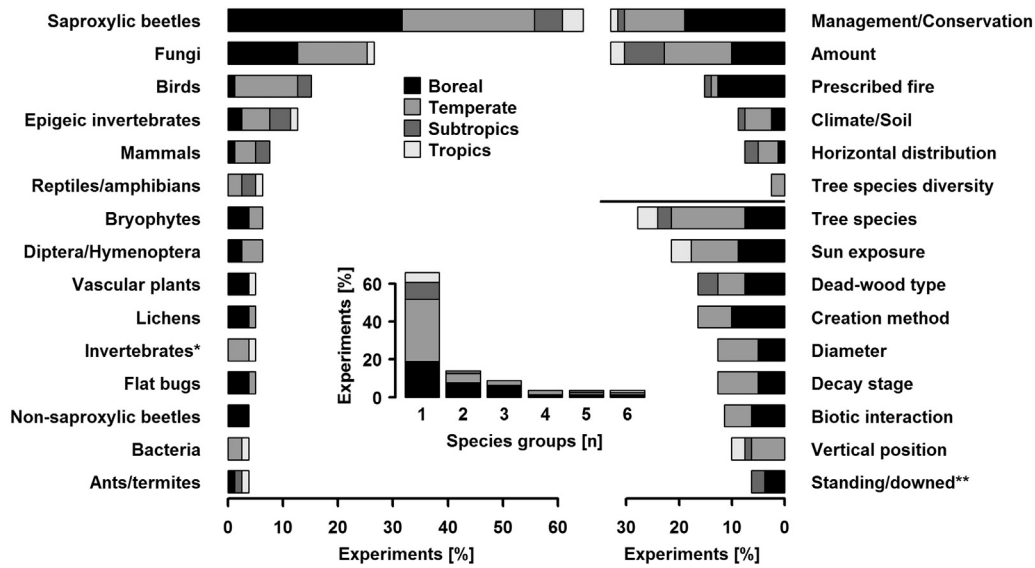


Fig. 3. Proportion of experimental studies targeting 1 of 15 species groups (left) or manipulating a factor at the biome, landscape or stand level (right, above the horizontal line) or at the object level (right, below horizontal line). *Various invertebrate taxa were grouped as invertebrates if no further classification was provided. **The factor standing/downed was also included in the factor dead-wood type. The inset shows the number of species groups studied per experiment.

of fuel wood or timber for domestic use by local populations. Studies focusing on management included, for example, the colonization of artificially exposed dead wood by saproxylic beetles in forest reserves and managed forests (Floren et al., 2014; Gibb et al., 2006a) or in landscapes with different histories of forest management (Kouki et al., 2012). The effect of prescribed burning to create or alter dead wood was mostly studied in the boreal zone (Hyvärinen et al., 2006; Toivanen et al., 2014). Artificial methods to create dead wood, such as cutting, topping, girdling or using explosives (e.g., Brandeis et al., 2002) and comparison to natural drivers, such as bark beetles attracted by pheromones (Shea et al., 2002), were studied mostly in the boreal and temperate zones.

3.2. Summary of results of experimental studies of dead wood

For our meta-analysis, we compiled 39 data sets on species richness. Our model revealed a significantly positive effect of the addition of dead wood on species richness of both saproxylic ($p < 0.001$) and non-saproxylic ($p < 0.01$) taxa (Fig. 4). Saproxylic taxa responded more strongly ($z = 3.40$) than non-saproxylic taxa ($z = 3.02$). Time after addition of dead wood had an overall positive effect ($z = 4.42$, $p < 0.001$). However, due to the low number of available studies, high variability of results of non-saproxylic taxa and potential publication bias, results regarding time and non-saproxylic species were unstable and have to be treated with caution (for details, see Appendix 1). Mean values of Hedges' d were 0.53 and 0.05 for saproxylic and non-saproxylic taxa, respectively. The strongest negative responses of non-saproxylic taxa (Fig. 4) were reported for lichen in a burned boreal forest (Hekkala et al., 2014) and for soil bacteria and litter-decomposing fungi in a tropical forest (Cantrell et al., 2014).

Across all species groups, climate, soil conditions and sun exposure affected species assemblages (Fig. 5, Table A2). Higher temperatures on the regional level (Müller et al., 2014) and higher amounts of sun exposure on the object level (e.g., Ranius et al., 2011) were related most frequently to higher richness or abundance of saproxylic insects, fungi, reptiles and amphibians. Negative effects of higher sun exposure were reported for fungi and molluscs (Lodge et al., 2014; Willig et al., 2014). The highest number of studies reported an increase in species richness or abundance of various taxa when dead wood was added, thus confirming the overall result of our meta-analysis. It is, however, important to note that there are some exceptions, most notably from a large-scale manipulative experiment conducted in the southeastern

USA. In that study, most invertebrate groups were unaffected by major additions or removals of dead wood (Ulyshen and Hanula, 2009a) and some vertebrates (e.g., snakes) appeared to be negatively affected by addition of certain types of dead wood (Owens et al., 2008). In other studies, the horizontal distribution of dead wood – clumped versus evenly spread – had contradictory effects depending on the studied species group (Barton et al., 2011; Kroll et al., 2012). Standing dead

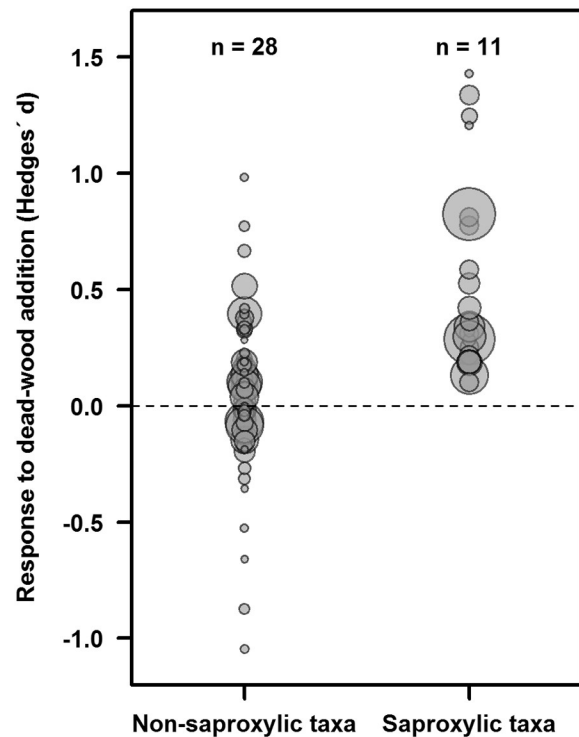
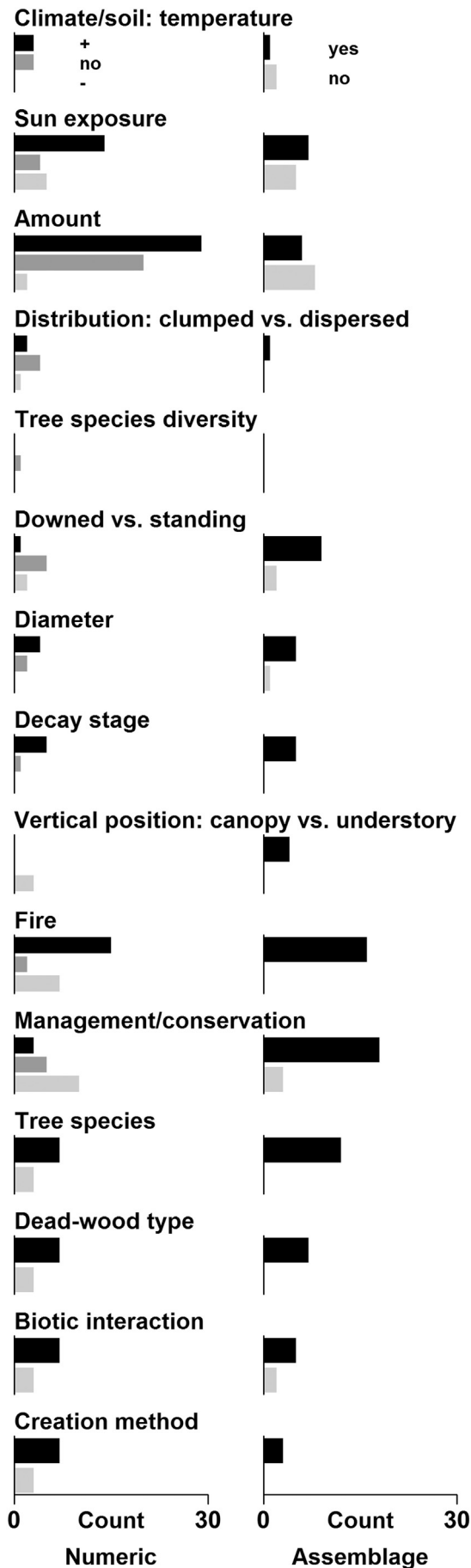


Fig. 4. Response of saproxylic and non-saproxylic taxa to the addition of dead wood. Positive values indicate higher mean species richness on plots with added dead wood than on controls; negative values indicate lower mean species richness on plots with added dead wood than on controls. For both groups of taxa, the effect of added dead wood was significant. The area of each point was scaled according to its weight in the meta-analysis. Several points were drawn from the same study when more than one year or one species group was studied.



wood was slightly more frequently reported to host fewer species than downed logs, but species assemblages differed strongly between the two orientation types (Jonsell and Weslien, 2003; Ulyshen and Hanula, 2009b), with some species, including red-listed ones, occurring only on snags (Gibb et al., 2006b). Similarly, assemblages of species frequently differed between types of dead wood in abundance or richness and in species composition. Species assemblages differed clearly between dead-wood objects of different decay stages or diameter, with generally more species in wood of advanced decay stages (e.g., Penttilä et al., 2013) and in larger logs (e.g., Grove and Forster, 2011), although the latter was rarely standardized by sampling area (Heilmann-Clausen and Christensen, 2004). Dead wood in the canopy hosted different assemblages of saproxylic beetles than dead wood near ground; the latter is colonized by more species (Gossner et al., 2013a). Communities colonizing different tree species differed frequently in terms of numbers and composition (Müller et al., 2015). Biotic interactions were best examined in the interplay of wood-decaying fungi and saproxylic beetles of the boreal and temperate zones and responses in abundance or richness and community composition were reported. Exclosure of insects by caging experimental dead wood clearly affected fungal assemblages, which shows that insect activity facilitates the colonization of dead wood by fungi (Strid et al., 2014). Likewise, decomposition by fungi creates species-specific dead-wood substrates that are then colonized by different saproxylic beetle assemblages (e.g., Jonsell et al., 2005).

Effects of forest management and conservation on biodiversity differed between studies, but a negative response of species richness to increasing forest management and differences in the species composition between stands of different management intensity have been reported most frequently, confirming the related meta-analysis of Paillet et al. (2010), which is based mostly on observational studies. In addition, an important large-scale experiment found richer assemblages of saproxylic beetles in areas with a short history of forest management (Kouki et al., 2012). Another study revealed that ranking of host tree species by local beetle communities is affected by management (Müller et al., 2015). Prescribed burning creates very specific dead-wood substrates and thus leads to clear differences in the species composition of burned and unburned forest for many species groups (Berglund et al., 2011). Fire further creates a pulse of new resource that favors some saproxylic taxa, particularly red-listed beetles, often leading to higher species numbers (Hyvärinen et al., 2006). Other taxa decrease in species richness or abundance after fire, e.g., lichens (Hämäläinen et al., 2014). Studies comparing different methods of creating dead wood showed that dead wood created artificially, e.g., topping, girdling or cutting, is colonized by saproxylic organisms and cavity-breeding birds, but dead wood created by natural agents, such as bark beetles, differs from such man-made substrates in terms of species composition and richness (e.g., Shea et al., 2002).

4. Discussion

4.1. The contribution of experimental studies to conservation

Overall, we detected a large number of experimental studies of dead wood covering all biomes, taxa and dead-wood factors. Our summary of the results demonstrated the potential of such experimental approaches

Fig. 5. Number of reported numerical differences in abundance, density, species richness or diversity (left), and differences in the composition of species assemblages (right) in relation to 15 factors of dead wood studied in the field experiments (for detailed results, see Table A2). For numeric, ordinal and two-level categorical variables, black indicates a positive response, light gray indicates a negative response and medium gray indicates no significant response. For multi-level categorical variables and effects on species assemblages, light gray indicates no significant difference and black indicates a significant difference. The same publication was counted several times when more than one species group was studied.

for providing relevant information on general ecological patterns of biodiversity in dead wood and for evaluating conservation and management activities. Results of experimental studies have complemented results of observational studies and contributed to the development of sophisticated conservation strategies for biodiversity associated with dead wood (e.g. Hutto, 2006; Müller et al., 2010; Similä and Junninen, 2012; Sverdrup-Thygeson et al., 2014a). One of the best examples comes from Finland and is based on more than 20 years of observational and experimental research (Similä and Junninen, 2012). The authors provide a synthesis of measures specific for different forest types which have been evaluated by numerous experimental studies. These measures include prescribed burning and creation of dead wood and gaps, and targets mostly restoration of protected areas but are also applicable for production forests (Similä and Junninen, 2012).

4.2. Dead-wood experimental studies are geographically biased

The worldwide distribution of experimental studies is clearly biased towards temperate and boreal forests of Europe and North America, as well as Australia. Results have been used to develop sophisticated dead-wood-oriented conservation strategies in these regions. No studies were found for Asian boreal forests and for temperate forests of South America and Africa, and only a few were found for temperate forests of Asia. An even more obvious lack of studies was that of tropical and subtropical forests of South America, Africa, India and Southeast Asia. However, as we conducted our search only in English, studies in other languages could have been overlooked. In the subtropics and tropics outside of North America, only a handful of experimental studies were conducted and these focused mostly on the preference of species for particular tree species (e.g., Tavakilian et al., 1997) or sun exposure (e.g. Schowalter et al., 2014). Also observational studies of dead wood in the subtropics and tropics are scarce (Grove, 2002b; Lachat et al., 2006), yet these regions hold some of the largest and most valuable forests with regard to biodiversity and ecosystem processes and services (Dirzo and Raven, 2003; Gaston, 2000; Shukla et al., 1990).

Tropical forests are seriously threatened by habitat fragmentation, forest degradation and conversion of natural forest to agro-industrial plantations or arable land (Dirzo and Raven, 2003; Hansen et al., 2008, 2010). Thus, in contrast to Europe, where conservationists are concerned with the quality of dead-wood habitats in managed forests rather than with forest clearance (Halme et al., 2013), in the tropics, the preservation of forest itself is the main issue and dead wood is of minor importance. This difference is underlined by the lack of experiments focusing on the widespread extraction of dead wood as fuel wood by local populations, which does not threaten the forest itself but may alter the amounts of dead wood significantly (Ribot, 1999). However, ongoing deforestation and forest degradation of tropical forests is likely to cause similar widespread regional extinctions of saproxylic species as witnessed in temperate and boreal regions of Europe (Grove, 2002a; Seibold et al., 2015). Thus, besides the conservation of pristine tropical forest, conservation strategies are needed in order to maintain saproxylic diversity in forests subject to selective logging, forest degradation and conversion to forest plantations (Basset et al., 2008; Grove, 2002b; Lachat et al., 2006, 2007; Tylianakis et al., 2007). For such strategies, there is an urgent need for research aimed at unraveling key relationships between habitat factors, management and biodiversity (Grove, 2002b). Experimental studies could evaluate, for instance, the host ranking of different tree species by saproxylic species (Müller et al., 2015) along a gradient of forest degradation or the effectiveness of dead-wood creation measures in degraded forests. Observational studies may produce important results regarding, e.g., necessary amounts and diameters of dead wood, more quickly than experiments.

4.3. Important taxa and late decay stages are underrepresented

Overall, saproxylic beetles were the best studied species group in experimental studies of dead wood and also a large number of field surveys focused on them (Grove, 2002a). Specific recommendations for conservation and forest management for saproxylic beetles could be derived from both types of studies, such as the importance of dead wood of large diameter (Grove and Forster, 2011) or of fire (Hyvärinen et al., 2006). Thus, conservation strategies targeting fauna associated with dead wood in boreal and temperate regions are based to a large extent on the information obtained for saproxylic beetles. The number of studies focusing on vertebrates was also rather high considering their comparatively low species number and their limited role in the decomposition process. Based on this information, a number of conservation strategies target vertebrate species, particularly birds, e.g., the white-backed woodpecker *Dendrocopos leucotos*, which are considered umbrella species for the conservation of dead-wood habitats, particularly snags (e.g., Arnett et al., 2010; Roberge et al., 2008).

Wood-inhabiting fungi were the focus of numerous field surveys and the results of these studies, combined with knowledge derived from experimental studies, have been considered in conservation strategies, particularly in Northern Europe (Junninen and Komonen, 2011). However, considering that wood-inhabiting fungi represent a large proportion of saproxylic biodiversity and are the main decomposers of wood (Boddy et al., 2008; Stokland et al., 2012), they are underrepresented in experimental studies of dead wood, especially in the tropics and subtropics. One reason for this might be that most research projects are funded for three to six years and thus, only few experimental studies follow the succession of dead wood for more than six years (Fig. 2, upper inset). In contrast to saproxylic beetles (Saint-Germain et al., 2007), the diversity of fungal fruiting bodies has its maximum at later decay stages, for example, after ten years in temperate forests (Heilmann-Clausen, 2001; Stokland et al., 2012). Thus, an essential part of the fungal succession on experimentally manipulated dead wood cannot be studied within the time span of most funding schemes by traditional surveys of fruiting bodies. However, fungal colonization starts readily on fresh dead wood (Heilmann-Clausen, 2001) and recently, sequencing fungal DNA from wood samples has become available which detect higher species numbers already at earlier decay stages compared to traditional surveys of fruiting bodies (Ovaskainen et al., 2013). Thus, molecular methods could complement surveys of fruiting bodies to study wood-inhabiting fungi.

Dead wood in late decay stages hosts different species assemblages of saproxylic taxa than early decay stages (Stokland et al., 2012). Thus, also late successional stages need to be studied to account for this portion of biodiversity. To reduce the costs of long-term projects, the time intervals between sampling events could be increasingly extended. As successional turnover slows down over time (Stokland et al., 2012), we suggest a logarithmic pattern with yearly sampling at the beginning of the experiment to cover rapid changes in early colonizing communities and longer time intervals during late decay stages. For short-term projects, we recommend using existing experimental setups at late decay stages instead of starting a new experiment to avoid high costs of dead-wood manipulation and to yield results more quickly. Our map of existing experimental studies (Fig. 2) and a list of all experimental studies identified in this review (Table A1) can help researchers to locate experimental studies that cover the factors of interest and are at the chosen stage of decay. In this way, a range of late successional species, such as fungi, bryophytes, lichens and some invertebrates, could be studied easily.

The high proportion of experimental studies that focused only on one species group underlines that most of these studies are not used to their full potential. For example, ants and termites have been largely overlooked in research on biodiversity in dead wood, despite being among the most abundant and influential arthropods in most subtropical and tropical terrestrial systems (Ulyshen, 2014; Wilson, 1971).

Saproxyllic Diptera and Hymenoptera contribute greatly to biodiversity and are involved in processes as, e.g., parasitoids or decomposers (Stokland et al., 2012). However, few experimental studies have focused on these taxa because of the shortage of taxonomists capable of identifying the high number of similar species. Particularly in less-studied regions, such as tropical forests, taxonomic knowledge is limited. Today, molecular methods such as DNA barcoding allow identification of large numbers of such cryptic taxa (Schindel and Miller, 2005) and could thus be more widely applied, particularly on existing experimental setups to complement the overall picture. Similar methods could also be applied for bacteria (e.g., Cantrell et al., 2014). By studying a broader range of taxa, conservation strategies can consider a larger portion of biodiversity and the role of these taxa in ecosystem functioning. In this way, unintentional negative effects of conservation measures on neglected species can be reduced.

4.4. Conservation and theory

Most experimental studies of dead wood intended to provide specific implications for conservation of saproxyllic species, as indicated by the high proportion of publications that focused on management rather than on general ecological theories. Such studies are important for evaluating and developing conservation strategies for specific forest types or regions and this is reflected by the implementation of results based on these studies in conservation strategies (e.g., Halme et al., 2013; Junninen and Komonen, 2011). Among the minority of studies that tested hypotheses based on ecological theories, the *species-energy hypothesis* was assessed most frequently (e.g., Barton et al., 2011). Such studies could most likely provide generalizable results that are not only valid for a certain region but can help to understand mechanisms behind observed pattern (Stephens et al., 2015). Such a deep understanding of ecological processes driving species' responses to management or environmental changes can help to evaluate and improve management or conservation strategies (e.g., Bässler et al., 2014). Therefore, besides evaluating specific management alternatives, general ecological concepts should be the backbone of future experimental studies.

The amount of dead wood was one of the most frequently studied factors in experimental studies of dead wood. Our meta-analysis confirmed the positive effects of dead-wood addition for saproxyllic species and is thus in line with an earlier meta-analysis based mainly on survey data (Lassaue et al., 2011). Although we included all available published data sets and a number of unpublished data sets, the data of our meta-analysis were biased towards the first years after addition of dead wood and are not numerous enough to further differentiate between non-saproxyllic taxa that are positively affected by dead wood amount and those that are negatively affected. Thus, the effect of dead-wood addition on non-saproxyllic taxa and in late decay stages should be further assessed. Results should be published also if responses were not significant. Although it was not analyzed if the number of saproxyllic species per specified area of dead wood increased with increasing dead-wood amount, in all studies included in our meta-analysis, saproxyllic species per plot responded positively to increased amounts of dead wood. The positive response of saproxyllic species underlines the importance of identifying threshold amounts of dead-wood required to maintain biodiversity; as have been developed for temperate and boreal forests based on observational studies (Müller and Bütler, 2010). Besides the required amount of dead wood, information is needed on whether standing or downed dead wood should be retained or created and how it should be distributed at both stand and landscape scales. The ability of observational studies to answer such questions is limited due to the variable nature of naturally-occurring dead wood with respect to frequency, size, age, etc.

Recent studies have found potentially important interactions between a number of factors, such as between dead-wood amount and temperature, which indicate that lower dead-wood amounts are

sufficient for maximum biodiversity in warm regions, whereas in cool climates, higher amounts are needed (Müller et al., 2014). This demonstrates how understanding such interactions can increase the efficiency of conservation strategies. Potential interactions that should be further disentangled concern, for example, dead-wood amount, diameter and type; tree species; and temperature and sun exposure. For instance, the species richness of assemblages in dead wood of a certain tree species might be higher when sun exposed, while that of another tree species might be higher when shaded (Müller et al., 2015). Besides interactions between dead-wood factors, an increasing number of observational and experimental studies including laboratory experiments have shown that biotic interactions between dead-wood colonizers are important for biodiversity and ecosystem functioning, such as decomposition (e.g., Fukami et al., 2010; Strid et al., 2014; Weslien et al., 2011). For instance, if priority effects of predecessor species or co-occurrence of species matter, this may determine the outcome of conservation campaigns (Weslien et al., 2011). To study such priority effects, again long-term studies or repetitions of old experimental studies including several taxa are needed.

4.5. Directing future experimental studies on dead wood

Our review shows that experimental approaches have contributed greatly to our understanding of biodiversity in dead wood and have provided crucial information for its conservation. Due to the complexity of the relationships that include a variety of taxa and dead-wood factors, interactions among them and geographical differences, there are still important gaps in knowledge and understanding of causal relationships. Considering the challenges experimental studies pose to researchers in terms of cost and study length, we derive the following recommendations for planning new experimental studies to use global capacities more efficiently:

1. To develop strategies for conserving saproxyllic organisms in tropical and subtropical forests subject to selective logging, forest degradation and transformation into plantations, new experimental studies should be established in these regions, possibly as collaborations between local researchers and researchers in industrial countries. Special attention should be given to conservation- and management-relevant factors and functionally important taxa, such as fungi, saproxyllic beetles and termites.
2. More studies should focus on saproxyllic communities associated with advanced stages of decomposition, most effectively by utilizing existing experimental setups, which can be identified using our map and list of existing studies.
3. Several functionally important, species-rich or conservation-relevant species groups are underrepresented in experimental studies of dead wood and should be the focus of future studies. Wood-inhabiting fungi, bryophytes or lichens would benefit from studies targeting advanced decay stages. Molecular methods could be applied to study cryptic but species-rich taxa, such as dipterans, hymenopterans and bacteria, as well as fungi during early decay stages.
4. More studies should focus both on disentangling interactions among dead-wood factors to improve conservation strategies and on biotic interactions between taxa that are relevant for conservation and ecosystem processes.
5. More studies should test hypotheses based on general ecological theories to provide more generalizable results for dead-wood ecology.

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Appendix A. Supplementary data

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