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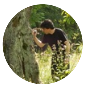

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Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood

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Summary

1. 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.

2. 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 forest plots. During the 3 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.

3. The composition of saproxylic beetle assemblages differed clearly between shady and sunny 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.

4. The stepwise 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.

5. *Synthesis and applications*. As canopy openness and habitat heterogeneity seem to be the major drivers of saproxylic beetle diversity in temperate forests, we recommend that managers 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.

Key-words: dead-wood enrichment, experiment, forest conservation, forest restoration, habitat-heterogeneity hypothesis, more-individuals hypothesis, saproxylic beetles, species-energy hypothesis, woody debris

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Introduction

The increase in species richness with increasing habitat area is among the most general patterns in ecology (MacArthur & Wilson 1967). The driving forces behind this relationship remain poorly understood, however, with possible explanations including energy availability, habitat heterogeneity, disturbance and population dynamics (MacArthur & Wilson 1967; Williamson 1988; Gaston 2000; Storch, Evans & Gaston 2005; Blakely & Didham 2010). For example, the 'more-individuals' hypothesis, a variant of the species-energy hypothesis, notes that the chemical energy (Clarke & Gaston 2006) available to all species increases with area, leading to more individuals and ultimately to more species (e.g. Wright 1983; Srivastava & Lawton 1998; Schuler, Chase & Knight 2015). Alternatively, the habitat-heterogeneity hypothesis suggests that the number of habitats increases with area and, as long as species use different habitats, species richness should also increase with area (e.g. Simpson 1949; MacArthur & MacArthur 1961; Tews *et al.* 2004). However, due to correlations between these potential determinants (Blakely & Didham 2010 and references therein), particularly between energy availability and habitat heterogeneity (Wright 1983; Whittaker 1998), it is difficult to assess the individual contribution of any single factor. Furthermore, the importance of the various factors might also change across taxonomic species groups or guilds. Nevertheless, to conserve biodiversity most efficiently, that is achieving benefits for the maximum number of species at restricted economic costs, it is important to manage only these factors that affect biodiversity of the species group under consideration.

One guild targeted by conservationists for which information on the drivers of biodiversity is of particular concern is saproxylic species, that is those directly or indirectly dependent on dead wood. Variation in the species richness of saproxylic organisms may be explained by both the species-energy hypothesis and the habitat-heterogeneity hypothesis (Seibold *et al.* 2015a). The former links saproxylic populations to the amount of dead wood, whereas the latter links the number of species to dead-wood diversity, that is resulting from differences in tree species, wood diameter, decay stage or sun exposure (Siitonen *et al.* 2000). In managed forests, dead-wood availability is generally lower than in natural forests (Grove 2002; Gossner *et al.* 2013b) as trees are harvested in a premature state (Lindenmayer, Laurance & Franklin 2012) and dead wood is frequently removed for use as fuel or to control pests (Lassauce, Lieutier & Bouget 2012; Thorn *et al.* 2014). Therefore, many conservation strategies recommend increasing the amount of dead wood in managed forests by retaining old, senescent and dead trees or logging residuals (Davies *et al.* 2007; Lindenmayer, Laurance & Franklin 2012) or by active measures to accelerate the development of dead wood in managed forests (Jonsson, Kruys & Ranius 2005; Davies *et al.* 2007; Bauhus, Puettmann & Messier 2009; Ranius *et al.* 2014). A recent meta-analysis has confirmed that active addition of dead wood increases biodiversity of saproxylic organisms (Seibold *et al.* 2015a).

Retaining or creating dead wood, however, creates economic costs because more wood remaining in the forest as dead wood means less marketable timber. As the majority of forest managers are forced to balance between economic and biodiversity requirements (Ranius *et al.* 2014), strategies have to optimize the benefits of conservation measures for biodiversity while limiting economic costs. Existing strategies that focus on increasing the amount of dead wood in managed forests could be improved by disentangling the role of dead-wood amount from that of dead-wood diversity. If dead-wood diversity has an independent effect on biodiversity of associated organisms, economic costs of conservation could be reduced by aiming at the lower boundary of recommended dead-wood amount (ranging from 20 to 60 m³ ha^{-1} in boreal and temperate forests; Müller & Bütler 2010) for maintaining a high species richness of saproxylic species while maximizing the diversity of woody substrates. However, under natural conditions, the amount of dead wood is correlated with dead-wood diversity, and thus, field studies based on survey data that used correlative analyses could not dissect the independent effects of the two variables on species richness (Müller & Bütler 2010).

Here, we experimentally exposed 800 m³ of logs and 5000 branches on shady and sunny forest plots in a montane mixed forest to disentangle the effects of dead-wood amount and dead-wood diversity on biodiversity of saproxylic beetles, which are one of the major groups involved in decomposing dead wood particularly during early stages of decay (Grove 2002; Müller *et al.* 2015b). We varied the amount and the combination of diameter classes of fresh coniferous and broadleaf dead wood, thereby covering gradients of dead-wood amount and dead-wood diversity, and sampled saproxylic beetles during the first 3 years. By stepwise analysis of abundance and species richness, that is species number corrected for abundance (Gotelli & Colwell 2001), we tested our predictions that (i) the abundance but not the richness of saproxylic beetle species increases with increasing dead-wood amount (more-individuals hypothesis, a variant of the species-energy hypothesis) and (ii) species richness increases directly with increasing dead-wood diversity (habitat-heterogeneity hypothesis).

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

The experiment was conducted in the montane zone of the Bavarian Forest National Park in south-eastern Germany (Fig. 1). In autumn 2011, overall, 190 0·1 ha plots were established in a randomized block design with five blocks across the study area (Seibold *et al.* 2014). Forests in the study area are characterized by a

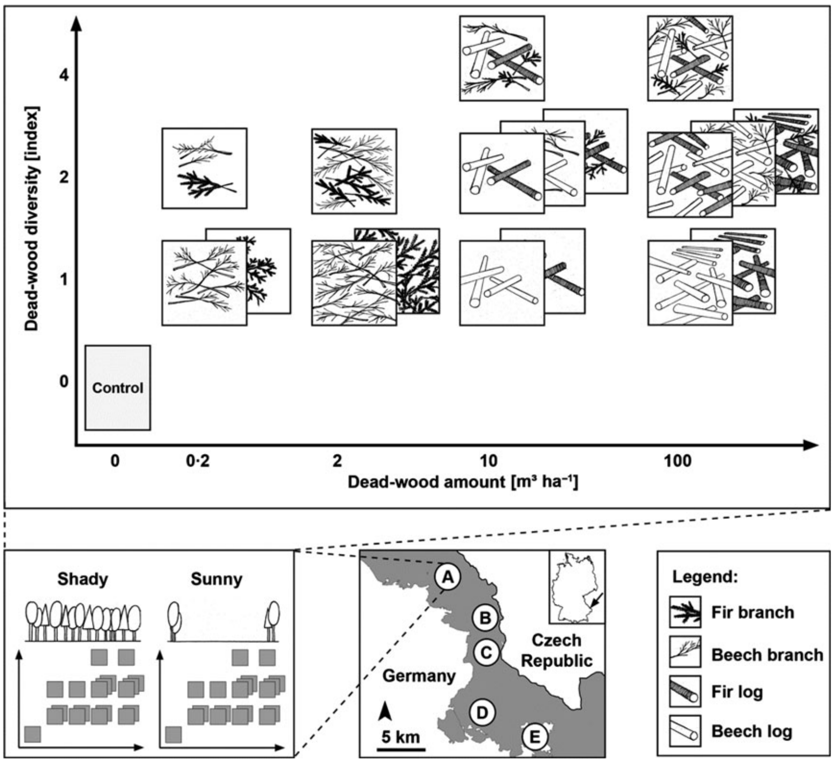

Fig. 1. Experimental set-up testing the effects of dead-wood amount (resource availability) and dead-wood diversity (habitat heterogeneity) relative to canopy openness on saproxylic beetles. Dead-wood diversity was characterized as number of different substrate types, that is tree species (European beech or silver fir) and diameter classes (branch or log), per plot following Siitonen *et al.* (2000). Nineteen combinations of dead-wood amount and dead-wood diversity were realized in both shady and sunny forest plots (bottom left) and replicated five times in a block random design (A–E; bottom centre), resulting in a total of 190 experimental plots. In the inset in the map, the black arrow indicates the location of the Bavarian Forest National Park in Germany.

mix of broadleaf and coniferous trees forming a small-scale mosaic of closed-canopy forest with sunny gaps created by bark beetles (Müller *et al.* 2010). In the buffer zone of the national park, where our plots were located, trees killed by bark beetles are removed by salvage logging and thus, the remaining amount of dead wood is similar to production forests. To account for effects of canopy openness (as a surrogate for 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 mature forest under a closed canopy (Fig. 1). To avoid canopy die-back due to bark beetles on our closed forest plots, the 0·1 ha plots were set up under a canopy dominated by European beech *Fagus sylvatica* (L.). The surrounding forest for both sunny and shady plots, however, contained significant amounts of both broadleaf and coniferous species with a slightly higher share of conifers surrounding open plots (mean basal area of broadleaf and coniferous trees within a radius of 300 m measured by single tree detection via LiDAR (Yao, Krzystek & Heurich 2012): sunny 4·5 vs. 10·8 m^2 ha^{-1} and shady 17·5 vs. 15·1 m^3 ha^{-1}). However, note that vital trees are not the actual source habitat of saproxylic beetles in our experiment.

Each plot was randomly assigned to one of 19 treatments designed to create gradients in amount and diversity of dead wood. The wood was cut less than 8 weeks before deposition and included logs (diameter: 25–50 cm, length: 5 m) of European beech and/or silver fir *Abies alba* (Mill.) and/or branches (diameter: 3–5 cm, length: 2–3 m) of one or both tree species. These tree species are naturally the dominant species in the montane zone of our study area. 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 m^3 ha^{-1} or 80 branches, about 2 m^3 ha^{-1}) or logs (4 logs, about 10 m^3 ha^{-1} or 40 logs, about 100 m^3 ha^{-1}) or a combination of logs and branches of low or high amounts (Fig. 1). To form a gradient of dead-wood diversity, we realized combinations of the different substrate types comprising three different levels of diversity. 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 the 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). To avoid strong shading by a dense grass layer on sunny plots, we mowed each plot once a year during the growing season. To characterize precisely the habitat amount per plot, we summed up the surface area of all logs and branches (Heilmann-Clausen & Christensen 2004). Following Siitonen *et al.* (2000), we calculated an index of dead-wood diversity as the number of different substrate types per plot ranging from 0 (no dead wood) to 4 (both logs and branches of both beech and fir).

SAMPLING OF BEETLES AND DATA PROCESSING

To sample flying and flightless beetles during the growing season, we installed two non-attracting flight-interception traps and two pitfall traps on each plot (Appendix S1, Supporting Information). 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. Two flight-interception traps have proved to yield the sufficient number of specimens required to obtain good correlations of diversity measures with local habitat conditions (Müller & Brandl 2009). Trapped beetles (283 243 individuals) were determined to the species level (1722 species; Table S1). Here, we analyse data of the first 3 years of the experiment.

From the data obtained, we separated saproxylic species according to reference lists (Schmidl & Bußler 2004) and pooled data for each plot and year to obtain representative assemblages for each plot (Müller & Brandl 2009). Species numbers of traps of the same plot and year were clearly correlated (2012: $r = 0{\cdot}74$, $P < 0{\cdot}001$; 2013: $r = 0{\cdot}77$, $P < 0{\cdot}001$; 2014: $r = 0{\cdot}80$, $P < 0{\cdot}001$; Fig. S1). A species was considered red-listed if it was categorized as indeterminate, restricted, near threatened, vulnerable, endangered or critically endangered according to the German Red List of Beetles (Schmidl & Büche 2015) or, if not in that list, then according to the regional Red List of Bavaria (Schmidl & Bußler 2004). For data-deficient species, a recently predicted red list status based on phylogeny and ecological traits was used if data for that species were available (Seibold *et al.* 2015b). We further classified species as conifer specialist, broadleaf specialist or generalist depending on the host tree required for larval development (Seibold *et al.* 2015b). For seven species (11 individuals), no red list status was available, and for one species (7 individuals), the host tree is currently unknown (Table S2). To serve as a non-saproxylic control group, we also extracted data on phytophagous beetle species of the families Elateridae, Chrysomelidae and Curculionidae (i.e. non-saproxylic species known to feed on green plant tissue or living roots).

STATISTICAL ANALYSES

All statistical analyses were conducted in R 3.0.2 (www.r-project.org). We applied non-metric multidimensional scaling (NMDS) using the function *metaMDS* in the add-on package *vegan* (Oksanen *et al.* 2009) for presence–absence data of all saproxylic species to characterize the composition of species assemblages (obtained stress value after 20 runs = 0·20). Treatment variables were fitted to the ordination *post hoc* using the function *envfit* with 1000 permutations. The first and second axes of the NMDS were further used as measures of species composition in our linear mixed models. Correlation coefficients of the scores of both axes with abundance and species number of saproxylic beetles indicated that the first axis includes differences in species composition that depend on abundance while the second axis was independent from abundance (Fig. S2). Non-metric multidimensional scaling was also applied to data of sunny and shady plots separately and the association between these ordinations was then compared by a permutation approach for Procrustean superimposition (Fig. S3) using the function *protest* with 1000 iterations (Peres-Neto & Jackson 2001).

As further response variables, we calculated the abundance and species number of all saproxylic species (Table S3), as well as the abundance and species number of red-listed species, conifer specialists, broadleaf specialists and generalists. Species without red list status or with unknown host tree associations were excluded from group-specific analyses. Furthermore, we retrieved the abundance and species number of phytophagous species. We identified indicator species for sunny and shady plots using the function *indval* in the add-on package *labdsv* (Dufrêne & Legendre 1997) with *P*-values adjusted for multiple testing (Benjamini & Hochberg 1995).

To test for effects of canopy openness (microclimate), dead-wood amount and dead-wood diversity, we fitted generalized linear mixed models with Poisson errors for count data and Gaussian errors for NMDS scores. In all models, we estimated fixed effects of canopy openness and – specifically for sunny and shady plots – of dead-wood amount (log-transformed surface area) and dead-wood diversity. All models included observation-specific random intercepts to account for overdispersion (Elston *et al.* 2001), and random effects of plot nested in block and year served to account for the nested design and temporal repetition on a plot. In the models of species richness, we used the log-transformed abundance as a control variable. The slope of the number of species vs. number of individuals showed no significant interaction with canopy openness or dead-wood amounts or diversity. For overall abundance and species richness, additional models evaluated differences of effects of changes in abundance and diversity of dead wood between years. We calculated the same models for a subset of plots ($n = 130$) and excluded plots that contained only branches and thus a lower overall amount of dead wood than when plots contained logs (Fig. 1). General biodiversity patterns were similar to those considering all plots (Table S4).

Results

We recorded 477 saproxylic beetle species (101 416 individuals). In the first year after exposure of the added dead wood, 387 saproxylic species (30 110 individuals) were trapped; 388 species (37 757 individuals) and 353 species (33 549 individuals) were trapped in the following 2 years. Overall, 68 red-listed species (4819 individuals) were recorded. Phytophagous species comprised 215 species (66 584 individuals) over all three sampling periods.

Overall, the composition of saproxylic species assemblages of sunny and shady forest plots was clearly distinct along the first NMDS axis ($P = 0{\cdot}001$ in *post hoc* fitting; Fig. 2). Furthermore, the overall species composition was significantly affected by year and by amount of dead wood ($P = 0{\cdot}015$ and $0{\cdot}001$, respectively), but not by dead-wood diversity. Analyses of indicator species confirmed the differences in species composition on shady and sunny plots; 105 and 57 characteristic species were identified on sunny plots and shady plots, respectively (Tables S5 and S6).

Linear mixed models revealed strong effects of canopy openness on the overall abundance and species composition (NMDS axes 1 and 2) of saproxylic assemblages and a marginally significant effect on species richness ($P = 0{\cdot}07$), with more individuals and species on sunny forest plots (Figs 2b,c and 3; for mean abundance and species number per treatment category see Table S3). Red-listed species, conifer specialists and generalists were more abundant and generalists and red-listed species were also more species-rich on sunny plots; broadleaf specialists were more abundant on shady plots (Fig. 4).

Increasing the amount of dead wood did not affect the overall abundance of saproxylic species, but positively affected overall species richness independently from abundance on sunny plots (Fig. 3). Red-listed species, generalists, and both conifer and broadleaf specialists positively responded to increasing dead-wood amounts on sunny plots (Fig. 4). The overall species composition (both

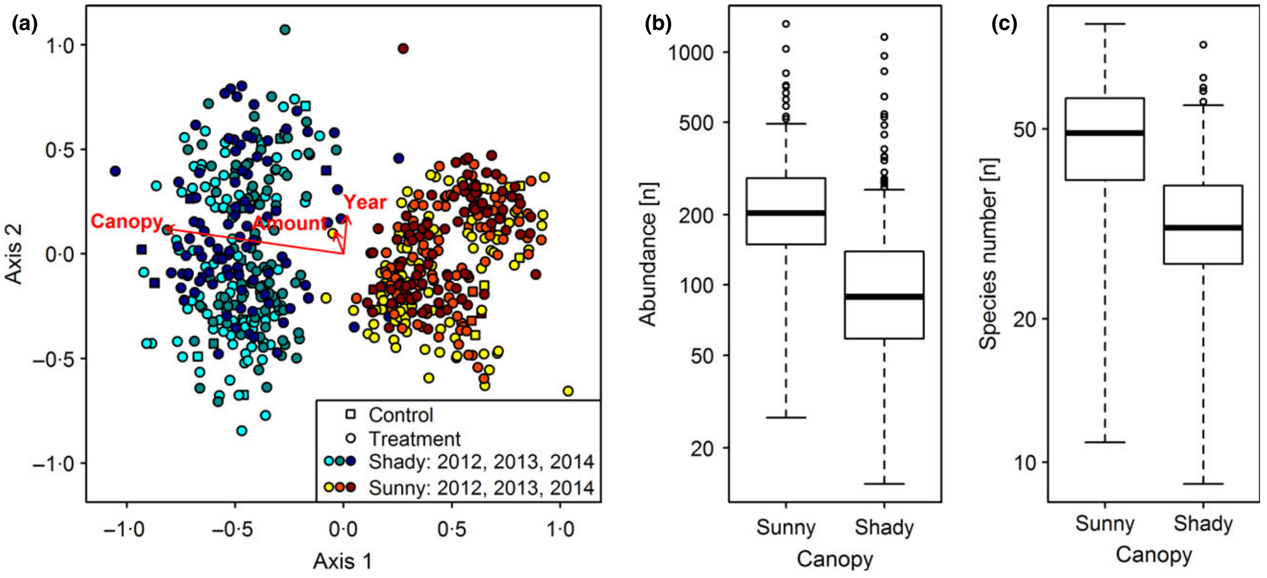

Fig. 2. (a) Ordination of species composition of saproxylic beetles in three consecutive years on 190 experimental plots with added dead wood according to nonmetric multidimensional scaling based on presence–absence data. The variables, canopy openness, year, amount of dead wood and diversity of dead wood were fitted to the ordination *post hoc* using the function *envfit* in vegan. Arrows indicate significant effects ($P < 0{\cdot}05$). (b) Abundance and (c) number of saproxylic beetle species on shady and sunny plots (note log scale of *y*-axis).

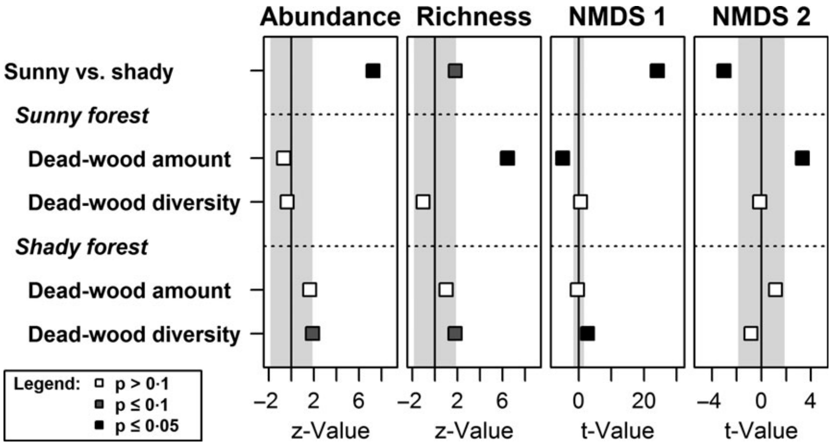

Fig. 3. Results of linear mixed models for abundance, species richness (Poisson error distribution) and measures of species composition of saproxylic beetle assemblages (NMDS axes 1 and 2; Gaussian error distribution) estimating the fixed effects of canopy openness and dead-wood amount and dead-wood diversity specific for sunny and shady plots. All models included observation-specific random intercepts to account for overdispersion, and random effects on plot nested in block and year to account for the nested design and repeated measurements in consecutive years. Species richness was modelled as number of species and included log-transformed abundance as a fixed effect (*z*-values not shown). Shaded areas indicate range of non-significant values (*t*- and *z*-values = ±1·96). Note the different limits and scales of the *x*-axes.

NMDS axes) was affected by dead-wood amount on sunny plots (Fig. 3). This effect was opposite in sign than the effect of canopy openness, which indicated increasing similarity to species composition on shady plots with increasing amounts of dead wood.

Dead-wood diversity positively affected both the overall abundance ($P = 0{\cdot}06$) and species richness ($P = 0{\cdot}07$) of saproxylic beetles on shady plots (Fig. 3), although the effects were only marginally significant. Species composition (NMDS axis 1) was also affected by dead-wood diversity on shady plots. In closed forests, red-listed species, generalists and conifer specialists were positively affected by dead-wood diversity (Fig. 4).

On sunny plots, the positive effect of dead-wood amount on species richness did not differ between years, whereas on shady plots, the amount of dead wood had a positive effect only in the third year (Table S7). The effect of dead-wood diversity on shady plots was highest in the first year. Abundance and species richness of phytophagous beetle species was lower on shady plots than on sunny plots, and abundance decreased with increasing dead-wood amount on sunny plots (Fig. 4).

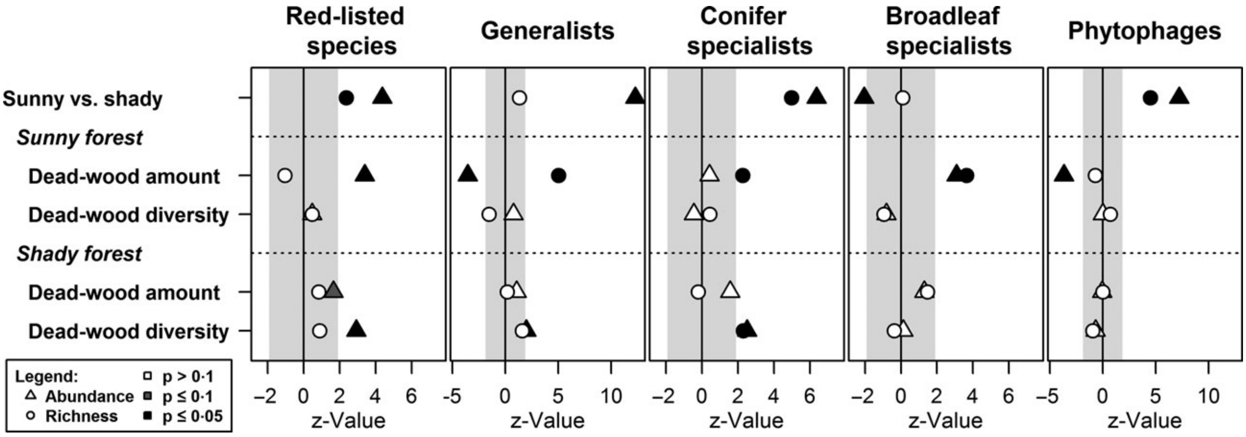

Fig. 4. Results of Poisson linear mixed models for abundance and species richness of saproxylic red-listed species, generalists, conifer specialists, and broadleaf specialists and phytophagous species estimating the fixed effects of canopy openness and dead-wood amount and dead-wood diversity specific for sunny and shady plots. All models included observation-specific random intercepts to account for overdispersion and random effects on plot nested in block and year to account for the nested design and repeated measurements in consecutive years. Species richness was modelled as number of species and included log-transformed abundance as a fixed effect (z-values not shown). Shaded areas indicate range of non-significant values (z-values = ±1·96). Note the different limits and scales of the x-axes.

Discussion

Overall, canopy openness was found to be the major driver of the diversity and composition of saproxylic beetle assemblages. Although the gradients of dead-wood amount and dead-wood diversity used in our study represented only a small portion of their natural range (Geiser 1994; Christensen *et al.* 2005), our experimental approach revealed independent positive effects of the two experimental factors on species richness of saproxylic beetles. These effects were, however, modified by canopy openness, as dead-wood amount played the main role on sunny plots and dead-wood diversity was more important on shady plots. The effect of dead-wood diversity is in line with the habitat-heterogeneity hypothesis. But, as dead-wood amount affected species richness (controlled for abundance) on sunny plots and not abundance, its effect cannot be explained by the more-individuals hypothesis which predicts increasing abundance with increasing resources. These results improve our understanding of the ecology of saproxylic beetles and may help to optimize dead-wood enrichment concepts in production forests.

Compared to other sampling methods, such as bark sieving or emergence trapping, flight-interception and pitfall traps collect a wider range of species, from those colonizing exposed dead wood to those crossing plots by chance and without affinity to the accumulated dead wood (Alinvi *et al.* 2006). Nevertheless, flight-interception traps are still the most useful sampling technique for characterizing local assemblages of saproxylic beetles (Hyvärinen *et al.* 2005; Gossner *et al.* 2013b), particularly when complemented with pitfall traps to sample flightless species (Müller & Brandl 2009). Furthermore, the control group in our study, phytophagous beetles, showed no significant response to addition of dead wood besides a negative effect of dead-wood amount on sunny plots. This can be attributed to the suppression of green biomass by dead-wood logs.

EFFECT OF CANOPY OPENNESS

Although observational studies have regularly found more saproxylic beetle species in sunny areas rather than in shady areas, such results are difficult to interpret because canopy openness and dead-wood amount are often correlated; both increase simultaneously when trees die during or after stand-replacing disturbances, for example bark beetle attacks (Bouget & Duelli 2004; Müller *et al.* 2010). However, few experimental studies that controlled for dead-wood amount by exposing equal amounts of dead wood under different microclimatic conditions have revealed positive effects of canopy openness (Vodka, Konvicka & Cizek 2008; Hjältén *et al.* 2012). We manipulated both canopy openness and dead-wood amount, and although we increased the local amount of dead wood greatly, only canopy openness affected the overall abundance of saproxylic beetles, and species richness was affected by both factors, albeit only marginally by canopy openness. Higher abundance and species richness of beetles in sunny habitats can be partly explained by the positive correlation between activity and temperature (Liu, Zhang & Zhu 1995). Note that a higher activity can increase the sampling efficiency of activity traps. However, temperature affects not only the activity of insects but also the rate of physiological processes (Clarke & Gaston 2006), with for example, shorter development phases under warmer conditions (Schowalter 2006). Thus, an increase in the abundance of insects with increasing temperature can be expected. Our results and the results of insect rearing experiments in dead wood exposed to warm or cold conditions (Vodka, Konvicka & Cizek

2008; Müller *et al.* 2015a) confirm this expectation as abundance and with it the number of saproxylic beetle species was higher in sunny than in shady areas including control plots (Table S3).

It is clear from our NMDS ordination and indicator species analysis that beetle communities in sunny vs. shady forest plots are compositionally distinct. Because we found canopy openness to marginally affect species richness even after controlling for abundance, we conclude that differences in species richness between shady and sunny forest plots were not solely due to differences in abundance. Despite some hypotheses, the mechanism for how temperature affects species richness independently from abundance is still under debate (Clarke & Gaston 2006). Several studies (e.g. Graham 1924; Vodka, Konvicka & Cizek 2008; Müller *et al.* 2010; Stokland, Siitonen & Jonsson 2012) as well as our results indicate that more saproxylic beetle species prefer sunny habitats. However, the preference for sunny or shady conditions seems to be unequally distributed among guilds (Müller *et al.* 2010) and possibly also across the phylogeny (Seibold *et al.* 2015b). In a large survey across the Bavarian Forest National Park, canopy openness positively affected abundance and richness of conifer specialists independently from dead-wood amount but had no significant effect on broadleaf specialists which were more associated with shady conditions and a high diversity of wood-decaying fungi (Müller *et al.* 2010). Although the amount of conifers surrounding our plots was higher for shady plots, we found higher abundance and richness of conifer specialists on sunny plots (Fig. 4, Table S6). Broadleaf specialists were more abundant on shady plots, thus confirming the survey results (Müller *et al.* 2010). This supports the view that the observed differences between beetle assemblages of shady and sunny plots are driven by microclimatic differences. To be more specific, further research needs to evaluate how host specificity of saproxylic beetles interacts with their microclimatic preferences (Müller *et al.* 2010, 2015b).

EFFECTS OF DEAD-WOOD AMOUNT AND DEAD-WOOD DIVERSITY

Attempts at identifying driving forces behind the species–area relationship have found support for the species-energy hypothesis or for the habitat-heterogeneity hypothesis depending on the system or taxonomic group under consideration. For instance, an experimental study using field microcosms found a clear effect of energy availability on species diversity when habitat heterogeneity was kept constant (Blakely & Didham 2010). In another interesting study, where habitat heterogeneity was not correlated with habitat area, habitat heterogeneity was identified as the most important predictor of species diversity (Báldi 2008). Some studies focusing on experimentally added dead wood have found positive effects of the amount of dead wood of the same type on abundance, species number and diversity of saproxylic beetles (e.g. Klepzig *et al.* 2012; Gossner *et al.* 2013a). Although our gradient of dead-wood diversity comprised only four different levels, richness of saproxylic beetles responded to dead-wood diversity even when controlling for abundance (Fig. 3). Thus, our second prediction based on the habitat-heterogeneity hypothesis that species richness increases directly with increasing dead-wood diversity is supported. In contrast to our first prediction, dead-wood amount did not drive the abundance of saproxylic beetles and with it the number of species, but directly affected species richness independently from abundance (Fig. 3). Such a direct effect of resource availability on species richness is not in line with the more-individuals hypothesis. One possible explanation of the observed pattern might include cryptic variation in dead-wood characteristics despite our manipulation of the diameter and species of dead wood. For example, temperature, wood density, water content, fungal colonization and decay stage can considerably vary within a single dead-wood object, particularly when of large size (e.g. Graham 1924; Saint-Germain, Buddle & Drapeau 2010; Leather *et al.* 2014), and thus cannot be manipulated. Therefore, the effect of dead-wood amount might include also an increase in the number of habitats, that is habitat heterogeneity, 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 could be attributed to habitat heterogeneity rather than resource availability. Regardless of the ecological mechanism behind the effect of dead-wood amount, increasing the amount of dead wood, particularly in the form of large logs or whole trees, supports more saproxylic beetle species and thus remains an important conservation measure.

The effects of dead-wood amount and dead-wood diversity were clearly mediated by canopy openness. Dead-wood diversity was the prevailing factor for biodiversity on shady plots and dead-wood amount prevailed on sunny plots (Figs 3 and 4). The lack of effect of dead-wood diversity on any of the response variables in sunny habitats may be due to lower colonization of branches on sunny plots, as we observed when we reared beetles from branch samples from sunny and shady plots (Appendix S4). In turn, higher dead-wood diversity promoted higher species richness and affected the assemblage composition of saproxylic beetles on shady plots. The stronger effect on species richness and species composition 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, that is having a dry and warm upper part and a cool and moist lower part (Fig. S4; Graham 1924), and thus, also caused by higher habitat heterogeneity with increasing amount of dead wood. This could be further pronounced by different volatile chemicals being emitted at different temperatures (e.g. Steckel, Knöpfle & Ohlmeyer 2013) and thus by a higher diversity of chemical cues attracting a higher variety of saproxylic beetle species in sunny habitats. On shady plots, the driver behind habitat heterogeneity shifted over the 3 years of the study from the diversity of added dead wood formed by the number of tree species and diameter classes to habitat heterogeneity within dead-wood objects, which increases with the amount of dead wood (Table S7). This can be attributed to decreasing differences between wood of different tree species (Stokland, Siitonen & Jonsson 2012) and advanced decomposition of branches, both of which reduce the diversity of the added dead wood over time, and also attributed to ongoing decomposition and with it increasing heterogeneity within and between logs. Red-listed species showed no response in species richness, but the positive response in abundance to dead-wood amount on sunny and marginally on shady forest plots, as well as to dead-wood diversity on shady plots (Fig. 4), indicates that populations of red-listed species would benefit from increasing these factors.

IMPLICATIONS FOR DEAD-WOOD ENRICHMENT STRATEGIES

In general, our finding that canopy openness and habitat heterogeneity are the major drivers of the diversity of saproxylic beetles is consistent with general ecological principles and indicates that conservation strategies world-wide should aim at providing high heterogeneity of dead wood, regarding, for example, tree species, diameter or cryptic variability within large logs, in open and closed forest conditions. More specifically for temperate montane mixed forests, which are often characterized by highly closed canopies and low amounts of dead wood, particularly of large diameters and of natural broadleaf species (Seibold *et al.* 2015b, and references therein), we derived four specific implications based on our results to improve conservation strategies for production forests and protected areas.

1. Dead wood is required in both sunny and shady forest habitats to maintain the full range of saproxylic species assemblages. Where natural gap formation is anthropogenically reduced, dead-wood creation should be realized particularly via gap felling.

2. Dead-wood diversity should be directly increased, particularly in shady forests, for example by selectively and repeatedly creating dead wood also of locally less abundant tree species and under consideration of the full range of diameters of different parts of trees.

3. In sunny forest stands, dead-wood amount should be increased to reach proposed thresholds, particularly in the form of large logs or whole trees comprising high habitat heterogeneity.

4. To compensate dead-wood habitat loss caused by logging, managers, who must deal with strong economic restrictions, should focus on providing a high diversity of dead wood (including the full range of diameter) while aiming at the lower boundaries of proposed dead-wood amount thresholds. Conservation managers should aim at high dead-wood amounts and dead-wood diversity by retaining or creating complete dying and dead trees.

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Data accessibility

Species list, R scripts and raw data are available from the online Supporting Information of this article.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Trap design and complete list of recorded species with red-list status and trait information.

Appendix S2. Supplementary results and mean abundances and species numbers per treatment category.

Appendix S3. Branch rearing data.

Appendix S4. Temperature inside dead-wood logs.

Appendix S5. R-code.

Appendix S6. Raw data.

Fig. S1. Scatterplots showing the number of species S in each of the two trap-systems (one flight interception and one pitfall trap) per plot for each of the three study years.

Fig. S2. Scatterplots showing the abudance N or number of species S and the scores of the first two NMDS-axes.

Fig. S3. Ordinations of species composition of saproxylic beetles on sunny and shady plots in three consecutive years on 190 experimental plots with added dead wood according to nonmetric multidimensional scaling based on presence–absence data.

Fig. S4. Histograms of temperature values measured over one year in sapwood and heartwood of dead-wood seven logs placed in sunny and shady forest plots.

Table S1. List of all trapped beetles determined to species-level with status as saproxylic or phytophagous and, for saproxylic species only, red list status and host-tree preference.

Table S2. Saproxylic species without red list status or host-tree trait.

Table S3. Mean and SD of abundance and species number of saproxylic beetles for each treatment category and year.

Table S4. Results of two generalized linear mixed models with a Poisson error distribution with the abundance and species richness of all saproxylic beetle species as response variable.

Table S5. List of saproxylic beetle species characteristic for sunny and shady forest stands as identified by indicator analysis with red list status (RL) and ecological traits (Seibold *et al*. 2015).

Table S6. Number and proportion of saproxylic beetle species with indicator value for sunny and shady forest stands categorized after larval feeding strategy and preferred host tree (Seibold *et al*. 2015).

Table S7. Results of two generalized linear mixed models with a Poisson error distribution with the abundance and species richness of all saproxylic beetle species as response variable.

Table S8. Estimates of the *z*-value (mean divided by standard error) of the fixed effects of a zero-inflated regression model with the number of saproxylic beetle individuals as response variable.